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BULLETIN

of CARNEGIE MUSEUM OF NATURAL HISTORY



EARLY TERTIARY ADAPSORICIDAE AND
ERINACEIDAE (MAMMALIA, INSECTIVORA)

OF NORTH AMERICA

LEONARD KRISHTALKA

NUMBER 1

PITTSBURGH, 1976

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EARLY TERTIARY ADAPISORICIDAE AND
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OF NORTH AMERICA

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Section of Vertebrate Fossils

BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY
Number 1, pages 1-40, figures 1-13, tables 1-7, appendix tables A,B,C

Issued June 16, 1976

Price: \$2.50 a copy

CONTENTS

Abstract	4
Introduction	4
Systematics	7
Family Adapisoricidae	7
<i>McKennatherium</i>	7
“ <i>Diacodon</i> ” <i>minutus</i>	10
<i>Scenopagus</i>	10
<i>Ankylodon</i>	16
<i>Macrocranion</i>	18
<i>Talpavus</i>	21
Adapisoricidae: Summary	26
Family Erinaceidae	28
<i>Litolestes</i>	28
<i>Leipsanolestes</i>	30
?Erinaceidae <i>Entomolestes grangeri</i>	32
Erinaceidae: Summary	32
Acknowledgements	33
References Cited	34
Appendix A	36
Appendix B	39
Appendix C	40

ABSTRACT

The differentiation and relationships among the four earliest known groups of lipotyphlan insectivores concerns the early Tertiary families Adapisoricidae, Erinaceidae, Nyctitheriidae and Geolabididae. The first two families compose the Erinaceomorpha and are considered here. North American adapisoricids comprise *McKennatherium* (*M. ladae*, and an undescribed new species), *Scenopagus* (*S. edenensis*, *S. priscus*, *S. curticens*), *Ankyledon*, *Talpavus* (*T. nitidus*, *T. duplus*, new species, *Talpavus* sp.), and *Macrocranium* (*M. nitens*). The erinaceids include *Litolestes* (*L. ignotus*, and tentatively, *L. lacunatus* and *L. notissimus*), *Leipsanolestes seigfriedti* and perhaps *Entomolestes grangeri*. *Leptacodon ladae* is here referred to *McKennatherium* and *Entomolestes nitens* to *Macrocranium*. "*Leptacodon*" *jepseni* and "*Diacodon*" *minutus* do not belong in their respective

genera. The former may be an adapisoricid. The latter is probably referable to *Adunator*, a European Paleocene condylarth.

McKennatherium, *Scenopagus*, *Talpavus*, and *Ankyledon* form a lineage of adapisoricids separate from *Macrocranium*, which may have originated in Europe, and which adds to the evidence of a Euramerican fauna during the early Eocene. *Litolestes ignotus* may be central to the radiation of later Tertiary erinaceids, and, along with *Ankyledon*, may have possessed five lower premolars—possibly a primitive character among erinaceomorphs. Adapisoricids and erinaceids share a common origin from a Cretaceous non-paleoryctid-leptictid group of insectivores, which may also have been basal to the radiation of primates, dermopterans, and ungulates.

INTRODUCTION

This study is an elaboration of part of a doctoral dissertation (Krishtalka, 1975) that concerned the systematics and relationships of the oldest known lipotyphlans: the Adapisoricidae, Erinaceidae, Nyctitheriidae, and Geolabididae. That project began as an effort to identify the insectivores from the Powder Wash local fauna, early Bridgerian of Utah, of which the adapisoricids are a mainstay of the discussions in this paper.

The systematics and relationships of the Order Insectivora are among the most perplexing and least understood problems in mammalian evolution. Many workers, among them Gregory (1910), Vandebroek (1961), Van Valen (1967), Thenius (1969), and most recently, Butler (1972) have attempted synthetic reviews of insectivore phylogeny and classification.

Insectivores were first regarded as a distinct group by Illiger (1811) and later divided by Haeckel (1866) into the suborders Lipotyphla and Menotyphla. The former comprised shrews, moles, and hedgehogs, or those insectivores that lack an intestinal caecum. The Menotyphla combined tree shrews, elephant shrews, and flying lemurs, or those animals in which a caecum did occur. Although the Menotyphla retain many primitive characters that are lost in the Lipotyphla, they are not a natural group. Flying lemurs and elephant shrews have been relegated to the separate orders Dermoptera (Gill, 1872) and Macroscelidea (Butler, 1956), respectively. The suggested relationships of the tupaiids have swung between primates and insectivores, and Butler (1972) favored an ordinal ranking (Scandentia) for them as well, at least until their affinities are better understood.

Romer (1966) grouped all fossil non-lipotyphlans

and some living menotyphlans as the Suborder Proteutheria, essentially a wastebasket taxon. Butler (1972) advocated retention of the Proteutheria, minus the living menotyphlans, as a separate order for the poorly understood fossil non-lipotyphlans, thus limiting the concept of the Insectivora to the Lipotyphla. The resultant Order Lipotyphla would include the living families Erinaceidae, Soricidae, Talpidae, Solenodontidae, Tenrecidae, and Chrysochloridae, and the extinct Adapisoricidae, Nyctitheriidae, Geolabididae, Nesophontidae, Micropternodontidae, Apternodontidae, and Plesiosoricidae. Butler's Order Proteutheria includes the Palaeoryctidae, Leptictidae, Apatemyidae, Pantolestidae, and Plagiomenidae.

Living lipotyphlans are united by the absence of an intestinal caecum, by a reduced jugal bone, an expanded maxilla in the orbital wall of the skull replacing the palatine, a mobile proboscis served by a series of muscles that affect the form of the skull, a reduced pubic symphysis, absence of the medial internal carotid artery, and an auditory bulla composed mainly of the basisphenoid (Butler, 1972). The fossil lipotyphlans are grouped together and with living forms mainly on the basis of dental evidence, although the known cranial remains also support affinities with the Lipotyphla.

Butler (1956, 1972) recognized a fundamental dichotomy among lipotyphlan insectivores—the Erinaceomorpha and Soricomorpha (Saban, 1954)—which he suggested may have originated in the Paleocene. The erinaceomorphs include the Adapisoricidae and the Erinaceidae. In these groups the infraorbital canal is long, the eye is large, and the coronoid process extends posterodorsally. The soricomorphs include the families Geolabididae, Nyctitheriidae, Soricidae, Talpidae, Ple-

siosoricidae, Dimylidae, Micropternodontidae, Solenodontidae, Nesophontidae and, tentatively, Apternodontidae. These groups possess a short, infraorbital canal, a small eye, and a more nearly vertical coronoid process (Butler, 1956; 1972; personal commun., 1975).

The amount of taxonomic shuffling of nyctitheres, geolabidids, adapisoricids, and erinaceids into various familial, subfamilial, and generic groupings in only the last decade is indicative of the poor understanding of the systematics of these early Tertiary insectivores. Biases of collecting and investigation are moot points in this problem. Most of the early work describing early Tertiary insectivore evolution stems from the study of single local mammalian faunas. Rarely did one investigator have at his disposal all of the pertinent fossil insectivore material from known early Tertiary localities. As a result, taxa were duplicated in the literature and their relationships remained muddled. This problem is magnified when considering relationships between North American and European insectivores (e.g., Russell, et al., 1975). Some recent work, however, has concentrated on the systematics of specific groups like nyctitheriids (Robinson, 1968a), geolabidids (McKenna, 1960b; Lillegraven and McKenna, 1975), and European adapisoricids (Russell, et al., 1975).

Remains of insectivores from the following localities were used in this study (see Fig. 1):

Torrejonian:

- (1) Gidley Quarry, Lebo Formation, Montana.
- (2) Rock Bench Quarry, Polecat Bench Formation, Wyoming.

Tiffanian:

- (3) Cedar and Silver Coulee Quarries, Polecat Bench Formation, Wyoming.
- (4) Mason Pocket, San Jose Formation, Colorado.
- (5) Bear Creek, Fort Union Series, Montana.

Wasatchian:

- (6) Four Mile localities, Wasatch Formation, Colorado.
- (7) Powder River localities, Wasatch Formation, Wyoming.
- (8) Big Horn Basin, Willwood Formation, Wyoming.
- (9) Lysite and Lost Cabin, Wind River Formation, Wyoming.
- (10) Huerfano localities, Huerfano Formation, Colorado.
- (11) Almagre localities, San Jose Formation, New Mexico.

Bridgerian:

- (12) Powder Wash, Green River Formation, Utah.
- (13) Bridger Basin, Bridger Formation, Wyoming.
- (14) East Fork, Tepee Trail Formation, Wyoming.

Uintan:

- (15) Myton Pocket, Uinta Formation, Utah.
- (16) Badwater localities, ?Tepee Trail Formation, Wyoming.

All measurements are given in millimeters. For those species represented by abundant material, only the observed range in size is presented in the tables, but measurements of each individual specimen appear in the appendices. Although the tooth nomenclature follows Van Valen (1967), Szalay (1969), and Krishtalka (1973), three terms used here in reference to the morphology of P_4^1 in early Tertiary lipotyphlans need further clarification: a premolariform P_4 is characterized by a large, dominant protoconid and an extremely short, usually unicuspid talonid. A small paraconid and metaconid may occur, but they are poorly differentiated from the protoconid.

On a semimolariform P_4 the talonid is much narrower than, but nearly as long as, that on M_1 , and usually bears two or three cuspules. The paraconid may be better developed than on a premolariform P_4 , but is lower than the metaconid and projects from the anterior part of the base of the protoconid.

A submolariform P_4 is essentially like M_1 , except for a narrower talonid and smaller cusps on the trigonid. Characteristically, the paraconid occurs at approximately the same height as the metaconid, and, in this regard, more closely approaches the condition on M_1 .

A premolariform P_4 bears only two cusps, a protocone and paracone. A semimolariform P_4 is more like M_1 in possessing a metacone as well.

The recent reclassification of mammals (McKenna, 1975) and its *raison d'être* pertains to this and other studies of mammalian phylogeny, especially those which are based almost exclusively on dental remains of fossil mammals and mammalian dental homologies. According to McKenna (1975), the primitive tokothere post-canine dental formula is $dP_1^1P_2^2P_3^3P_4^4dP_5^5M_1^1M_2^2$, in which $dP_5^5M_1^1M_2^2$ have conventionally been referred to as $M_1^1M_2^2M_3^3$, respectively. Recent suggestions of the occurrence of five premolars in *Litolestes*-like erinaceids, *Plagiomene*-like dermopterans (Schwartz and Krishtalka, 1976), and some plesiadapiform-tarsiiform

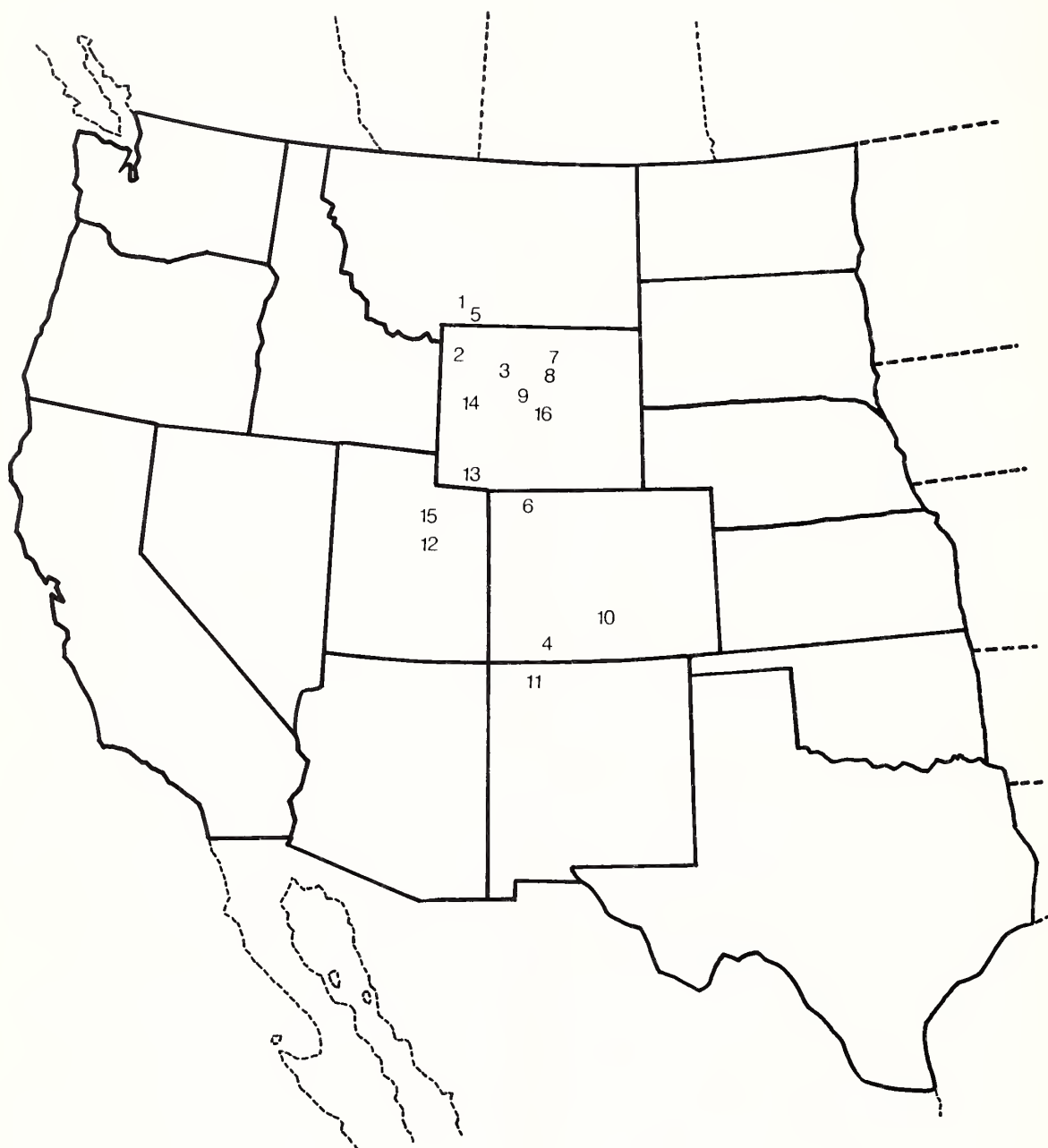


Fig. 1. Geographic location of localities of early Tertiary insectivores described in this paper.

primates (Schwartz and Krishtalka, 1976; Schwartz, in press)—groups that also have three molars—may require an emendation of the dental formula proposed as primitive for tokotheres. A moot point is the homology of the fourth tooth in the lower jaw—the alleged “premolariform canine”—in *Litolestes ignotus* and *Plagiomene multicuspis*. This problem is discussed in detail in Schwartz and Krishtalka (1976) and in the sections in this paper dealing with *Litolestes* and *Ankylodon*.

The use of the conventional P_{1-4}^1 in this paper is a nomenclatorial compromise. Few of the known early Tertiary erinaceomorphs are represented by adequate dental remains necessary to establish dental homologies. *Litolestes* and *Ankylodon* are exceptions, although the deciduous or permanent nature of each of the putative five premolars is uncertain. Also uncertain are the homologies of the premolars in those erinaceomorphs that have four, and the loci involved in the

reduction to four premolars from the suggested primitive complement of five.

The abbreviations used in this paper are as follows:

AMNH, American Museum of Natural History
CM, Carnegie Museum of Natural History
PU, Princeton University
TTU, Texas Tech University
UCM, University of Colorado Museum
UCMP, University of California Museum of Paleontology
YPM, Yale Peabody Museum
L, length
W, width
AW, anterior width (width of trigonid)
PW, posterior width (width of talonid)

All photographs are stereoscopic scanning electron micrographs and present occlusal views.

SYSTEMATICS

Family Adapisoricidae (Schlosser, 1887)

Schlosser (1887) erected this family of insectivores to include the European Paleocene genera *Adapisorex* (Lemoine, 1883) and *Adapisoriculus* (Lemoine, 1885). Simpson (1928) added *Entomolestes* and *Leipsanolestes* to this group and relegated *Adapisoriculus* to the marsupials, although the latter has since been identified as a tupaiid (Van Valen, 1965a). Later, Simpson (1945) abandoned the concept of the Adapisoricidae and regarded *Adapisorex* as a leptictid, *Entomolestes* as an erinaceid, and *Leipsanolestes* as a subgenus of *Leptacodon*. Van Valen (1967) revived and broadened the Adapisoricidae to include four subfamilies (Adapisoricinae, Geolabidinae, Nyctitheriinae, Creotarsinae), but acknowledged that many of the generic allocations were tentative. The nyctitheres (Robinson, 1968a) and geolabidines (Butler, 1972) were subsequently removed from the Adapisoricidae and raised to familial rank, an action with which Novacek (in press) and I agree. The Creotarsinae, as Van Valen (1967) acknowledged, is not a natural group.

Of the genera originally assigned by Van Valen to the Adapisoricidae, only the following (in addition to *Ankylodon*) are here recognized as belonging to that family: *McKennatherium* (including *Leptacodon ladae*), *Scenopagus*, *Talpavus*, and *Macrocranion* (including *Entomolestes nitens*, *Aculeodens*, and *Messelina*). *Ses-*

pedectes and *Proterixoides* may also belong here or in the Erinaceidae. Both genera are currently under investigation elsewhere (Novacek, MS). Butler (personal commun., 1975) and I believe that the genus *Adapisorex*, upon which the family is based, is an erinaceid. *Diacodon minutus* may be a condylarth, and is discussed in detail in this paper.

A number of European forms from the Paleocene and Eocene (*Amphilemur*, *Gesneropithec*, *Amphidotherium*, *Adunator* and *Paschatherium*) that previously had been referred by some authors to the Adapisoricidae have recently been shown to lack affinity with this family of insectivores (Russell, et al., 1975).

McKennatherium Van Valen, 1965b

McKennatherium libitum, named by Van Valen (1965b) as a new genus and species of paromomyid primate, was later shown to be a junior synonym of *Leptacodon ladae* (Szalay, 1968). Van Valen (1967) correctly suggested that *L. ladae* and the genotype of *Leptacodon*, *L. tener*, warranted generic distinction, a point overlooked by Russell, et al. (1975) in their review of North America adapisoricids. Accordingly, *McKennatherium* is a valid genus, although not a primate. Its systematics have never been formalized, nor its relationships described. *M. ladae* is here identified as a primitive Torrejonian adapisoricid, very near the ancestry of *Scenopagus*.

McKennatherium ladae (Simpson, 1935),
new combination
(Fig. 2; Table 1)

Leptacodon ladae Simpson, 1935

McKennatherium libitum Van Valen, 1965b.

TYPE: USNM 9640, RP₄-M₃, Gidley Quarry, Fort Union Formation, Montana.

REFERRED SPECIMENS: AMNH 35954, RP₃-M₃; and tentatively PU 14774, LP₃-M₁; PU 14776, RP₂, P₄, M₂₋₃; PU 14780, LP₄-M₂; PU 17722, LP₃-M₃; PU 18500, LP₃-M₃; PU 19836, RP₄-M₂.

LOCALITIES: Gidley Quarry, Fort Union Formation, Montana; Rock Bench Quarry Beds, Polecat Bench Formation, Wyoming.

KNOWN DISTRIBUTION: Torrejonian of Montana and Wyoming.

DESCRIPTION: P₂ and P₃ are double rooted. P₂ is essentially a tall, asymmetrical, elongated cusp with a long, concave, posterior slope and a shorter, convex, anterior slope. A minute cuspule occurs at the base of the posterior slope, and a tiny lingual ridge at the base of the anterior one.

P₃ is dominated by a high, nearly symmetrical protoconid. A tiny paraconid occurs on the anterior part of the base of the protoconid. The talonid is very short, and consists of a single cuspule that is separated from the posterior face of the trigonid by a labiolingual groove.

P₄ of *M. ladae* is semimolariform, with a tall protoconid, a slightly lower metaconid on its lingual face, a low, anterobasal paraconid, and a basined talonid. The talonid is approximately one-half of the width of the trigonid, bears three cusps, and has a straight posterior margin. The paraconid varies in size and in the degree of separation from the anterobasal part of the protoconid.

The lower molars of *M. ladae* are very *Scenopagus*-like, especially resembling *S. curticens*. Character-

istically, the paraconid is compressed to a strong lophid that extends lingually from the protoconid, and is appressed to the anterior face of the metaconid. The paraconid and the metaconid are closer, and the anteroposterior compression of the trigonid is greater on M₂₋₃ than on M₁. The protoconid and metaconid are conical, almost bulbous cusps. The talonid is approximately as wide as the trigonid on M₁, but extends less labially on M₂₋₃. The hypoconulid is medial, and on M₃ projects posteriorly from the elongated talonid. The hypoconid wears flat on M₁₋₃, the entoconid remains high, and the cristid obliqua meets the trigonid labial to the protoconid-metaconid notch. M₃ is reduced in *M. ladae* as it is in *S. curticens* and *S. priscus*.

REMARKS: The molars on the Princeton specimens are slightly wider than on AMNH 35954 and are tentatively referred to *M. ladae*, until a larger sample is available.

M. ladae clearly differs from Paleocene *Leptacodon sensu stricto* (i.e., *L. tener*, *L. packi* and *L. munusculum*) in the lophid-like paraconid and compressed trigonid on the lower molars, the more robust, bulbous cusps, a more external cristid obliqua, and a hypoconid that becomes flat with wear.

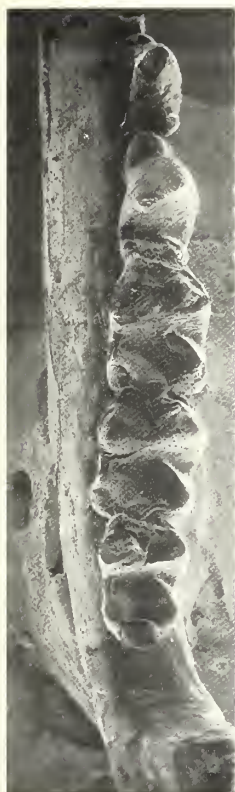
A new and larger species of *McKennatherium*, based on material in the Princeton collection from Rock Bench, Polecat Bench Formation, Wyoming, will be described elsewhere.

The molars of *McKennatherium* are virtually identical in cusp morphology to those of *Scenopagus*. However, P₄ in *McKennatherium* is semimolariform, whereas that of *Scenopagus* is premolariform. Premolarization of P₄ may be a characteristic trend in lineages of erinaceomorphs (Clemens, 1973), and is implied in the

Table 1. Dimensions of lower teeth of *McKennatherium ladae*

	P ₄		M ₁			M ₂			M ₃		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
AMNH 35954	1.5	0.9	1.6	1.2	1.2	1.5	1.2	1.2	1.6	1.1	0.9
PU 14774	1.8	1.1	1.7	1.4	1.3	—	—	—	—	—	—
PU 14776	1.6	1.0	—	—	—	1.7	1.3	1.4	1.7	1.3	1.0
PU 14780	1.6	1.1	1.7	1.3	1.3	1.6	—	1.4	—	—	—
PU 17722	1.6	1.0	1.7	1.3	1.3	1.7	1.4	1.3	1.6	—	0.9
PU 18500	1.7	1.1	1.7	1.4	1.4	1.7	1.5	1.4	1.8	1.3	1.0
PU 19386	1.6	1.0	1.7	1.2	1.2	1.8	1.4	1.3	—	—	—
Mean	1.63	1.03	1.68	1.30	1.28	1.67	1.36	1.33	1.68	1.23	0.95

Fig. 2. *McKennatherium ladae*. (A) AMNH 35954, RP₃-M₃, Fort Union Formation, Montana: approx. X 10; (B) PU 17722, LP₃-M₃, Polecat Bench Formation, Wyoming, approx. X 12. Fig. 3. "*Diacodon*" *minutus*, PU 19395, RP₃-M₃, Polecat Bench Formation, Wyoming, approx. X 12.

**2
A****2
B****3**

transition from *McKennatherium* to *Scenopagus*. *McKennatherium* appears to be a primitive Torrejonian representative of an adapisoricid lineage that included the species of the Eocene *Scenopagus* and *Ankylodon*.

“*Diacodon*” *minutus* Jepsen, 1930
(Fig. 3)

The generic and familial status of this species is in doubt, having been referred to the leptictids *Diacodon* (Jepsen, 1930) and *Palaeictops* (Gazin, 1956), and to *Leptacodon*, ?Metacodontidae (McKenna, 1960a). Some investigators (C. B. Wood; K. Rigby, personal commun., 1974, 1975) have noted that “*D.*” *minutus* is similar in some respects to hyopsodontid condylarths.

The type of “*D.*” *minutus* was recovered from the Silver Coulee Beds, Polecat Bench Formation, late Tiffanian, of Wyoming. Additional material referable to this species is known only from the type locality and the older, early Tiffanian, Cedar Quarry beds of the Polecat Bench Formation.

“*Diacodon*” *minutus* is not a species of the leptictids *Diacodon* or *Palaeictops* or of the nyctitheriid *Leptacodon*. Its lower dentition is virtually identical to the type of *Adunator lehmanni* (Wa 368) from the Tiffanian Walbeck fauna of Europe (Russell, 1964), an observation also noted by Russell and C. B. Wood (personal commun., 1975). However, the known parts of the upper dentition of “*D.*” *minutus* are not quite as similar to those of *Adunator*. Relative to *Adunator*, M₁₋₂ of “*D.*” *minutus* are more transverse, with taller, more nearly conical cusps, a deeper labial emargination, and a weaker hypocone. A problem inherent in this comparison is the degree of certainty of association of the upper and lower dentitions in each of the two taxa.

In the original description of “*D.*” *minutus*, Jepsen (1930) stated that the remains of the upper and lower dentitions were associated, inasmuch as they were found inches apart. The association of upper and lower teeth of *Adunator* is less convincing (Russell, 1964). Although Russell (1964; *in* Russell, et al., 1975) originally identified *Adunator* as a leptictid, his recent restudy of the genus indicates that its affinities lie more with the condylarths (C. B. Wood, personal commun., 1975)—a conclusion I reached independently concerning “*D.*” *minutus* (Krishtalka, 1975).

The lower molars of *Adunator*-“*D.*” *minutus* are also similar to those of the adapisoricid *McKennatherium ladae*, except for a number of moot features: the talonid on M₁₋₂ is slightly elongate, and M₂ is

larger than M₁. The paraconid on M₂ is extremely compressed and is merged with the anterior face of the metaconid. The metaconid, in turn, is greatly expanded anteriorly, in lingual view, so that it is much larger and more bulbous than the protoconid. These exceptions to adapisoricid affinities in the lower molars of *Adunator*-“*D.*” *minutus* are features associated with some Tiffanian hyopsodontid condylarths like *Haplaletes*. However, the molars in *Haplaletes* have much lower crowns and are more nearly bunodont and robust.

P₄ in *Adunator*-“*D.*” *minutus* is submolariform, with a well-developed paraconid as high as the metaconid. As such, P₄ differs from the semimolariform P₄ of *McKennatherium*, and is closer to P₄ of *Haplaletes*. Similarly, the paraconid is strong on P₃ in “*D.*” *minutus*, weaker in *Haplaletes*, and absent from P₃ of *McKennatherium*. On the basis of the lower dentition alone, *Adunator*-“*D.*” *minutus* appear to be adapisoricid-like hyopsodontids, and may be congeneric.

Scenopagus McKenna and Simpson, 1959

After McKenna and Simpson (1959) described *Scenopagus mcgrewi* as a new erinaceid insectivore, McGrew (1959) and McKenna (1960a) noted that a number of the species included by Matthew (1909) in *Nyctitherium* warranted generic separation and bore specific resemblance to *Talpavus* and *Scenopagus*. Following these suggestions, Robinson (1966, 1968a) referred *Nyctitherium priscum* and *N. curticens* to *Scenopagus priscus*, and arrangement accepted by Russell, et al. (1975). Earlier, Robinson (*in* McKenna, et al., 1962) had advocated the synonymy of the leptictid *Diacodon edenensis* (McGrew, 1959) with *Scenopagus mcgrewi* and combined the two as *S. edenensis*. Thereafter, *Scenopagus* material recovered from Bridgerian and Late Wasatchian localities (Robinson, 1966; McGrew and Sullivan, 1970; West, 1973) was referred either to the larger *S. edenensis* or to the smaller *S. priscus*. Examination of the sample of *Scenopagus* from Powder Wash and the Bridger Formation now allows clearer definition of the species of *Scenopagus* and the ancestry of the late Eocene and Oligocene *Ankylodon*.

Scenopagus edenensis (McGrew, 1959)
(Fig. 4; Tables 2, 3)

TYPE: AMNH 55685, P₄-M₃, Tabernacle Butte, Bridger Formation (Upper), Wyoming.

REFERRED SPECIMENS: P₄: TTU-P- 7145, 7146, 7147, 7148, 7149. M₁: TTU-P- 7150, 7151, 7152, 7153, 7154, 7155, 7156, 7157, 7158, 7159, 7175. M₂: TTU-P- 7170, 7171, 7172, 7173,

7174, 7176, 7177, 7178, 7179, 7167, 7168, 7169. M³: TTU-P-7190, 7191, 8232, 8233, 8234. DP⁴: TTU-P-8235, 8236, 8237, 8238, 8239, 8240, 8241, 8242, 8243. M₁: TTU-P-7161, 7162, 7163, 7164, 7165, 7166. M₂: TTU-P-7180, 7181, 7182, 7183, 7184, 7185, 7186, 7187. M₃: TTU-P-7188, 7189. CM 13739, LP₄-M₁; CM 13732, RM₂₋₃; CM 13734, RP₂-M₁; CM 13728, RM₂₋₃; CM 6449, RM₁₋₃; CM 13731, RM₁; CM 13740, RM₂; CM 6444, LP₃-M₁; CM 6441, RP₄, M₁; CM 17318, RP₃-M₁; CM 13737, LP₄; CM 13730, RP₂, P₄-M₂; CM 13729, LM₁₋₂; CM 13735, LP₄; CM 6485, RP₂-M₂; CM 13733, LM₂; CM 13736, M₃; CM 13738, RP₄; CM 6443, RM₂₋₃; CM 17317, RM₂₋₃; CM 13741, P₄-M₂; CM 6433, P₄-M₂; YPM 13612, LM₃; YPM 16910, RM₂₋₃; YPM 14934, LM₁₋₂; YPM 14932, RM₂; YPM 16911, RM₁; AMNH 11428, RM₁₋₂; TTU-P-5571, RM₁₋₂; TTU-P-5572, LM₂₋₃.

LOCALITIES: Powder Wash, Green River Formation, Utah; Dry Creek, Lone Tree, Henry's Fork, Phil Mass Ranch, Bridger Formation (Upper), Wyoming; Grizzly Buttes, Black's Fork, Bridger Formation (Lower), Wyoming; Lost Cabin, Wind River Formation, Wyoming; locality III, Huerfano Formation, Colorado.

KNOWN DISTRIBUTION: Bridgerian, Wyoming; late Wasatchian, Wyoming and Colorado.

DESCRIPTION: Much of the lower antemolar dentition is preserved on CM 13730, CM 6485, CM 17318, and CM 13734, partial mandibles from Powder Wash. P₁ and P₂ are single-rooted, essentially unicuspid teeth, with an incipient paraconid on the antero-lingual face of the protoconid, and a tiny cingular heel. P₃ is double-rooted and lacks a metaconid. The paraconid is not a distinct cusp, but a flange projecting from the anterolingual part of the base of the large rounded protoconid. A paracristid extends from the apex of the protoconid to the paraconid flange. The talonid, which is extremely short, is developed as a weak labiolingual ridge separated by a narrow groove from the posterior wall of the trigonid. A tiny cuspule (?hypoconid) occurs on the talonid ridge and is linked to the trigonid by a faint crest (?cristid obliqua).

P₄ is premolariform, with a prominent trigonid and a shorter, unicuspid talonid. The base of the talonid is wider than the trigonid, but the dorsal width of the talonid, from the cristid obliqua to the internal edge of the crown, spans only the lingual one-third of P₄. The protoconid is the major cusp of the trigonid. A small, conical paraconid arises from the anterolingual part of the base of the protoconid. The two cusps are linked by a paracristid, and share a continuous, curving, labial-antrolabial face, but are demarcated lingually by a shallow, vertical notch. The metaconid, on the lingual face of the protoconid, is approximately one-half the height of the latter and slightly higher than the paraconid. The cristid obliqua is short and extends directly posteriorly from the trigonid to a

small hypoconid. The entocristid slopes downward, lingually and forward from the hypoconid to the posterolingual part of the base of the trigonid, and completes enclosure of the shallow-basined talonid. Characteristically, a deep furrow occurs on the external wall of the talonid from the cristid obliqua to the base of the crown.

The lower molars of *S. edenensis* lean lingually and are essentially rectangular in occlusal outline, with a slight constriction between the talonid and trigonid. The trigonid, approximately one-third higher than the talonid, is wider than the talonid on M₂₋₃ but is as wide as, or narrower than, the talonid on M₁. M₃ is unreduced, has an elongate talonid, and is longer than M₁ or M₂. The protoconid and metaconid are high, rounded cusps, barely compressed anteroposteriorly, with the metaconid slightly larger and taller. The paraconid is not a distinct cusp. Rather, it is compressed into a strong, broad paracristid that runs lingually from the anterior part of the base of the protoconid and ends anterior to and merged with the base of the metaconid. Characteristically, in lingual view the notch between the paracristid and metaconid is much higher than the talonid notch at the junction of the entocristid and base of the metaconid. In *Macrocranion* (= *Entomolestes nitens*) the paracristid notch is only slightly higher than, or at the same level as, the talonid notch. The trigonid on M₁ of *S. edenensis* is less compressed anteroposteriorly than on M₂₋₃, and is more nearly triangular.

The talonid basin on M₁₋₃ is deep, the hypoflexid shallow. The cristid obliqua is strong and meets the trigonid wall labial to the ventral notch between the protoconid and metaconid. The entoconid is the highest and sharpest of the talonid cusps and is rarely worn, whereas the hypoconid is lower and more nearly rounded, becoming flat with wear. The hypoconulid, smaller than, and distinct from, the entoconid and hypoconid, occurs only slightly lingual to the midline, and on M₃, projects posterodorsally.

Two mental foramina occur in *S. edenensis*: one below P₄ and the other below the anterior root of P₃.

P₃ through M² of *S. edenensis* have been adequately described elsewhere (McKenna and Simpson, 1959). Isolated M³s identified from Powder Wash are narrower and shorter than M², possess a strong, flaring parastylar salient, and lack a hypocone. As on M¹⁻², the protocone on M³ is compressed anteroposteriorly, and the conules are evident, but fairly small. The buccal edge of the crown, oriented anterolabially, is defined by a weak ectocingulum, and, unlike M¹⁻², is



4
A



4
B



4
C



not emarginate. The paracone, much larger and higher than the extremely reduced metacone, is linked to the tip of the parastylar salient by a weak preparacrista. Small, short anterolingual and posterolingual cingula occur basal to the protocone.

A number of isolated DP₄s have tentatively been identified from the Powder Wash collection, based on morphological and size association with known parts of the dentition of *S. edenensis*. DP₄s thought to pertain here are molariform teeth, triangular in occlusal view and much longer buccally than lingually, relative to P₄, M¹⁻². The paracone and metacone are rounded and conical, with the paraconid slightly taller and larger. The protocone and the conules are sharp, crescentic cusps with equally distinct proto-cristae and conulecristae. As on M¹, the ectoflexus is shallow, and the posterior cingulum is developed as a broad shelf that terminates in a hypocone lingual and basal to the protocone. However, the hypocone is much smaller relative to M¹⁻², and the lingual contour of the crown is continuous. On M¹⁻² of *S. edenensis*, a valley occurs lingually between the bases of the protocone and hypocone. A small parastyle occurs on the parastylar salient of DP₄, which juts anteriorly beyond the remaining anterior margin of the crown. As on P₄, M¹⁻², the post-metacrista is developed as a high crest running from the metacone to the tip of the expanded metastylar salient. A preparaconulecrista extends to the parastyle and defines a narrow paracingulum along the base of the paracone. Similarly, the postmetaconulecrista delineates a strong metacingulum along the posterior part of the base of the high postmetacrista.

REMARKS: The distinctions between *S. edenensis*, *S. priscus*, and another species, *S. curticensis*, are discussed in the next two sections. The large sample of *S. edenensis* from Powder Wash (early Bridgerian) exhibits a range of variation that excludes AMNH 56035, holotype of "*S. mcgrewi*" (late Bridgerian), and raises the question of the validity of the synonymy of *S. mcgrewi* and *S. edenensis* (see Table 3). Along with AMNH 56035, left maxilla with P³-M², McKenna and Simpson (1959) tentatively referred AMNH 56034, partial left lower jaw with M₃, to *S. mcgrewi*. Both specimens were recovered from the same excavation in the Bridger Formation, near Tabernacle Butte. The authors contended that the lower jaw with M₃ was suitable in size and structure for occlusion with the

maxilla. In the same paper, Simpson noted that the holotype of *Diacodon edenensis* (McGrew, 1959), a lower jaw with M₁₋₃, resembled *Scenopagus* more than the leptictid *Diacodon*, although its occlusal fit with the holotype maxilla of *S. mcgrewi* was poorer than that of the referred jaw of *S. mcgrewi*. Robinson (in McKenna, et al., 1962) concurred with Simpson concerning the affinities of *Diacodon edenensis* and referred that species to *Scenopagus*. However, Robinson discounted as individual variation Simpson's observed differences between the lower jaw of *S. mcgrewi* and *D. edenensis*, and synonymized all the material as *Scenopagus edenensis*. The large sample of *S. edenensis* from Powder Wash makes it difficult to attribute to individual variation alone the rather large difference in size between the type maxilla of *S. mcgrewi* and the upper limit of the size range of the upper dentition of *S. edenensis*, although the tentatively referred lower jaw of *S. mcgrewi* (AMNH 56034) falls within the upper limit of the range in size of M₃ of *S. edenensis*. Two alternative answers are suggested: The tentatively referred lower jaw of *S. mcgrewi* is actually *S. edenensis*, and AMNH 56035 remains the type and only known specimen of *S. mcgrewi*; or the large range in variation of the lower dentition of *S. edenensis* is artificial and actually represents two distinct populations. There is some basis for the latter suggestion. The type material of *S. mcgrewi* and *S. edenensis* was recovered from deposits in the upper part of the Bridger Formation. The referred sample of *S. edenensis* came from the early Bridgerian Green River Formation. Examination of the measurements of lower dentitions referred by Robinson (1966) and West (1973) to *S. edenensis* shows that specimens recovered from the Upper Bridger deposits fall within the upper part of the size range, whereas those from the Lower Bridger horizons, as well as those from the temporally equivalent Powder Wash locality, make up the lower part of the size range. Thus, the Upper Bridger material may represent typical *S. edenensis*, whereas that from lower Bridgerian and equivalent localities may represent a smaller population of *S. edenensis*, or a smaller species of *Scenopagus*. Unfortunately, almost all remains of upper dentition referable to *Scenopagus* have been recovered from early Bridgerian horizons in Wyoming and Utah. Apart from the type maxilla of *S. mcgrewi*, only West (1973) has reported upper teeth of *Scenopagus* from Upper Bridger localities,

◀ Fig. 4. *Scenopagus edenensis*, Green River Formation, Utah. (A) CM 17318, RP₃-M₁, approx. X 12; (B) CM 6449, RM₁₋₃, approx. X 12; (C) CM 6433, LP₄-M₂, approx. X 14.

and these correspond well to the size range of upper teeth from Powder Wash that are here identified as *S. edenensis*. Except for size, all material from early and late Bridgerian horizons referred here and elsewhere to *Scenopagus edenensis* and *S. mcgrewi* is structurally identical. Consequently, all the material is referred to *S. edenensis*, although we may be dealing with a series of temporal subspecies from the Late Wasatchian through the Late Bridgerian.

Scenopagus priscus (Marsh, 1872)
(Fig. 5; Tables 2, 3)

TYPE: YPM 13509, Bridger Formation, Wyoming.

REFERRED SPECIMENS: P₄: TTU-P- 7051; M₁: TTU-P- 7060, 7078, 7075, 7074, 7077, 7062, 7073, 7080, 7076, 7059, 7057, 7053, 7066, 7068, 7065, 7055, 7069, 7071, 7056, 7072, 7079, 7064, 7067, 7070, 7063, 7061, 7058; CM 30784; M₂: TTU-P- 7101, 7102, 7116, 7112, 7106, 7109, 7107, 7115, 7108, 7113, 7110, 7114, 7103, 7104, 7111, 7105, CM 30783; M₁: TTU-P- 7094, 7098, 7099, 7097, 7096, 7100, 9082, 7092, 7093, 7081, 7083, 7085, 7090, 7095, 7087, 7086, 7088, 7120, 7121, 7119; M₂: TTU-P- 7124, 7125, 7117, 7118, 7089, 7122, 7129, 7131, 7132, 7130, 7126, 7127; M₃: TTU-P- 7128, 7123, 7137, 7140, 7138, 7139, 7135, 7142, 7134, 7141, 7143, 7136. CM 13753, LP₄-M₁; CM 13749, LM₁₋₂; CM 13750, RP₄-M₁; CM 13744, P₄; CM 17316, M₂₋₃; CM 13746, LM₁; CM 13743, LM₂₋₃; CM 13748, M₁₋₂; CM 6486 RP₄-M₂; CM 17319, LM₂₋₃; CM 13751, LP₄-M₂; CM 13752, LP₄-M₁; AMNH 56060, LM₁₋₃; AMNH 55156, LP₄-M₁.

LOCALITIES: Locality III, Huerfano Formation, Colorado; Powder Wash, Green River Formation, Utah; Henry's Fork and Hyposodus Hill, Bridger Formation (Upper), Wyoming.

KNOWN DISTRIBUTION: Late Bridgerian, Wyoming; early Bridgerian, Utah; late Wasatchian, Colorado.

DESCRIPTION AND REMARKS: *S. priscus* closely resembles *S. edenensis* in known parts of the dentition, but is much smaller and bears a number of diagnostic differences in cusp morphology. On P₄ of *S. priscus*, the paraconid is flange-like and the talonid is usually narrower than the trigonid. M₃ of *S. priscus* is much reduced relative to M₂, the ectoflexus on M₂ is deep, and the lingual groove between the bases of the hypocone and protocone on M₁₋₂ is weak. In contrast, the paraconid on P₄ is more nearly cuspidate and distinct in *S. edenensis*, and the talonid is generally wider than the trigonid. M₃ of *S. edenensis* is unreduced, but elongate relative to M₂. The labial emargination of M₂ is relatively shallow, and the lingual indentation between the bases of the hypocone and protocone on M₁₋₂ is pronounced.

McGrew and Sullivan (1970) first described putative upper teeth of *S. priscus*. Although these teeth from Bridger A are very similar to upper molars of *S. priscus* from Powder Wash, they are significantly larger and are here referred to *S. curticens*, a species of *Scenopagus* described below. Apart from size, the M₁s and M₂s discussed by McGrew and Sullivan differ from *S. priscus* in possessing a more pronounced indentation between the bases of the hypocone and protocone, and a shallower emargination of the labial border of the crown.

AMNH 11488, previously referred to *S. priscus* (Robinson, 1966), is here and elsewhere (Russell, et al., 1975) identified as *Talpavus nitidus*. The latter authors also referred AMNH 55156 from Huerfano to *Talpavus* sp. In contrast to *Talpavus*, P₄ on AMNH 55156 bears a basined talonid. I follow Robinson (1966) in retaining that specimen in *S. priscus*. The distinctions between *Scenopagus* (especially *S. priscus*) and *Talpavus* are described below in the section dealing with the latter genus.

The type of *S. priscus*, listed by Robinson (1966: Table 4) as YPM 15309, should read YPM 13509.

Scenopagus curticens

(Matthew, 1909), new combination

(Fig. 6; Tables 2, 3)

Nyctitherium curticens Matthew, 1909

TYPE: AMNH 12055, partial left mandible with M₁₋₃, from Henry's Fork locality, Bridger Formation (Upper), Wyoming.

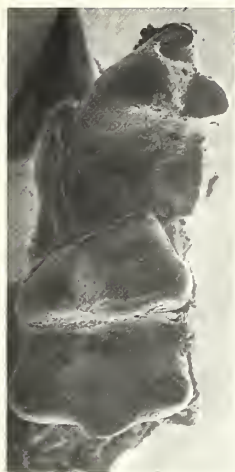
REFERRED SPECIMENS: YPM 15254, RP₄-M₃; YPM 16913, LM₁₋₂; YPM 14939, LM₁₋₂; YPM 13610-a, RP₄; YPM 13610-b, LP₄-M₂; YPM 13610-2, LM₁₋₂; YPM 15255, LM₂₋₃; YPM 16912, LP₄-M₁; YPM 16914, RM₂; AMNH 12058, RM₂₋₃; AMNH 12062, LM₁₋₃; AMNH 12064, RP₄-M₁; AMNH 11491, RM₁; AMNH 59643, RM₁; AMNH 48183, RP₄, M₂; TTU-P- 3928, RM₁₋₃; TTU-P- 7054, RM₁; UCMP 96155, LM₁₋₃.

LOCALITIES: Henry's Fork, Twin Buttes, Lone Tree, and Dry Creek, Bridger Formation (Upper), Wyoming; North Leavitt Ranch, Bridger Formation (Lower), Wyoming; unknown localities, Bridger Formation, Wyoming; Cattail Spring, and Point Gulch, Bridger Formation (Upper or Lower), Wyoming; Quarry 88, Almagre facies, San Jose Formation, New Mexico; Alheit Quarry, Hiawatha Member, Wasatch Formation, Colorado; Friars Formation, California.

KNOWN DISTRIBUTION: Bridgerian, Wyoming; Wasatchian, New Mexico; early Wasatchian, Colorado; early Uintan, California.

DESCRIPTION: The type and referred specimens exhibit features characteristic of *Scenopagus*, but morphologically intermediate between *S. edenensis* and

Fig. 5. *Scenopagus priscus*, Green River Formation, Utah (A) CM 13752, LP₄-M₁, approx. X 20; (B) CM 13749, LM₁₋₂, approx. X 15; (C) CM 17319, LM₂₋₃, approx. X 14; (D) CM 30784, RM₁, approx. X 12 (E) CM 30783, LM₂, approx. X 12. Fig. 6. *Scenopagus curticens*, Bridger Formation, Wyoming. (A) YPM 15254, RP₄-M₃, approx. X 12; (B) YPM 16914, RM₂, approx. X 10.



**5
A**



**5
B**



**5
C**



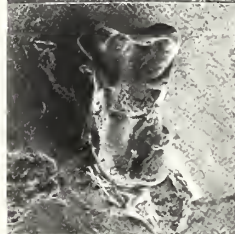
**6
A**



**5
D**



**5
E**



**6
B**



Table 2. Dimensions of lower teeth of *Scenopagus edenensis*, *S. curticens* and *S. priscus*

	P ₄			M ₁			M ₂			M ₃	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>S. edenensis</i>	2.0- 2.4	1.4- 1.6	2.1- 2.4	1.7- 1.9	1.7- 2.0	2.1- 2.7	1.8- 2.2	1.8- 2.0	2.2- 2.7	1.7- 1.8	1.2- 1.5
Mean	2.06	1.48	2.23	1.80	1.83	2.25	1.96	1.84	2.38	1.72	1.34
N.	10	9	13	13	12	22	19	19	19	9	9
SD.	0.8		0.12	0.09	0.16	0.22	0.14	0.11	0.35		
CV.	3.93		5.78	5.07	9.01	9.79	7.41	5.97	14.79		
<i>S. curticens</i>	1.5- 1.6	1.1- 1.2	1.7- 2.0	1.4- 1.6	1.5- 1.6	1.7- 1.9	1.5- 1.7	1.4- 1.6	1.5- 1.7	1.2- 1.3	0.9- 1.2
Mean	1.52	1.18	1.82	1.49	1.53	1.77	1.58	1.46	1.60	1.26	1.04
N.	6	6	11	11	14	12	11	12	5	7	5
SD.			0.07	0.08	0.07	0.06	0.10	0.12			
CV.			3.88	6.00	4.78	3.79	6.32	8.24			
<i>S. priscus</i>	1.2- 1.4	0.9- 1.1	1.3- 1.5	0.8- 1.3	0.9- 1.3	1.4- 1.6	1.1- 1.3	0.8- 1.2	1.3- 1.5	0.8- 1.1	0.6- 0.8
Mean	1.30	0.96	1.43	1.04	1.11	1.45	1.20	1.04	1.33	0.95	0.72
N.	6	7	31	31	29	18	18	17	15	15	12
SD.			0.07	0.07	0.06	0.06	0.07	0.03	0.04	0.07	0.05
CV.			5.40	7.23	5.87	4.09	6.39	3.39	3.48	7.92	7.25

S. priscus. As in *Scenopagus*, the paraconid and metaconid on the premolariform P₄ are lower than (and merged with) the protoconid, and the talonid is essentially unicuspid, short and basined. On M₁₋₃ the paraconid is compressed into a low, broad paracristid, and the metaconid and protoconid are large, rounded cusps, with the metaconid slightly taller. The cristid obliqua originates labially on the posterior wall of the trigonid. The hypoconid, lower than the high, conical entoconid, becomes flat with wear and the hypoconulid occurs lingual to the midline. The talonid extends farther labially than the trigonid on M₁, but is narrower than the trigonid on M₂₋₃. Two mental foramina occur on the mandible, one below P₄ and P₃, respectively.

S. curticens is intermediate in size between *S. priscus* and *S. edenensis*, but is closer to *S. priscus* in the smaller, less cusp-like nature of the paraconid on P₄, a talonid narrower than the trigonid on P₄, and a reduced M₃ relative to M₂. Also, the single M² referred here to *S. curticens*, and the upper molars de-

scribed by McGrew and Sullivan (1970) as *S. priscus*, are virtually identical to upper molars of *S. priscus*, except that they are larger and possess a deeper valley between the lingual faces of the hypocone and protocone, and a shallower labial emargination.

YPM 13610-a, 13610-b, and 14939, previously referred to *S. priscus* (Robinson, 1966) are here placed in *S. curticens*.

REMARKS: *S. edenensis*, *S. curticens*, and *S. priscus* were contemporaneous during the Bridgerian and Late Wasatchian. Only *S. curticens* has been recognized from earlier deposits. The reduction of the M₃ in *S. curticens* and *S. priscus* may be a derived feature, relative to the retention of an unreduced M₃ in *S. edenensis*. With premolarization of P₄, the species of *Scenopagus* could have radiated from a Paleocene adapisorid like *McKennatherium ladae*.

Ankylodon

The genus *Ankylodon* is known from the Late Eocene (Setoguchi, MS thesis) and Oligocene [(Galbreath,

Table 3. Dimensions of upper teeth of "*Scenopagus mcgrewi*," *S. edenensis*, *S. curticens* and *S. priscus*

	p ⁴		M ¹		M ²		M ³	
	L	W	L	W	L	W	L	W
" <i>S. mcgrewi</i> "	2.8	3.3	2.8	3.7 est.	2.5 est.	3.9		
<i>S. edenensis</i>	2.0	2.6- 2.9	2.1- 2.4	3.0- 3.3	2.0- 2.2	3.1- 3.5	1.5- 1.9	2.6- 2.8
Mean	2.0	2.69	2.25	3.18	2.10	3.31	1.67	2.73
N.	6	7	8	11	6	7	3	3
SD.				0.09				
CV.				2.66				
<i>S. curticens</i>					1.5	2.5		
<i>S. priscus</i>	1.4	2.0	1.4- 1.6	1.9 2.2	1.1- 1.4	1.9- 2.2		
Mean			1.47	2.06	1.32	2.09		
N.	1	1	15	17	6	7		
SD.			0.07	0.07				
CV.			4.81	3.64				

1953; Lillegraven and McKenna, (MS); Patterson and McGrew, 1937)] of North America. Excellent material comprising most of the upper and lower dentition of a Chadronian species of *Ankyledon* is presently being described by Lillegraven and McKenna (MS). The authors have kindly allowed me access to the manuscript and casts of the material. The dental morphology of *Ankyledon* mirrors that of *Scenopagus* as follows: P₁ and P₂ are single-rooted and unicuspid. P₃ and P₄ are double-rooted, possess a large protoconid, a small paraconid, and a short, shallow-basined talonid with a tiny hypoconid. A metaconid is lacking on P₃ and is present, but lower than the protoconid on P₄. The talonid is wider than the trigonid on M₁ but narrower on M₂₋₃. On M₁₋₃ the paraconid is anteroposteriorly compressed into a strong low paracristid, the metaconid is taller and larger than the protoconid, the cristid obliqua is labial on the posterior wall of the trigonid, the hypoconid is lower than the high conical entoconid, and becomes flat with wear, and the hypoconulid occurs slightly lingual to the midline. On M₃ the talonid is elongate, and the hypoconulid projects posterodorsally.

As in *Scenopagus*, P₄ of *Ankyledon* lacks conules and bears a tall, central paracone, a lower lingual protocone, a small hypocone on the postprotocrista, a small anterior parastylar salient, a large metastylar expansion, and a high postmetacrista. The crown is essentially T-shaped with an anteroposteriorly expanded lingual end. M₁₋₂ are very transverse, with a large valley separating the bases of the hypocone and protocone lingually. The postcingulum is strong and shelf-like and bears a large hypocone. The postmetacrista is high, the buccal margin of the crown is deeply emarginate medially, and the stylar salients are expanded. M₃ lacks a hypocone, is smaller than M₂, and possesses a large paracone and an extremely reduced metacone.

As Russell, et al. (1975) also noted, the features that distinguish *Ankyledon* from *Scenopagus* are not unique, but represent the elaboration of certain characters in *Ankyledon* beyond the condition seen in *Scenopagus*. Compared to *Scenopagus*, P₁ of *Ankyledon* is relatively higher, but P₂ is reduced. P₃ possesses a taller protoconid, a more distinct paraconid, and a longer, wider, better-developed talonid. Similarly, on P₄, the proto-

conid and metaconid are higher and more conical. The paraconid, although not cuspsate, is much larger and projects more anteriorly from the base of the trigonid, and the talonid is more elongate. On M_{1-2} of *Ankylodon*, the trigonids are more anteroposteriorly compressed, the protoconid and metaconid are taller, sharper cusps; the talonid is longer, the hypoflexid is deeper, and the cristid obliqua is more arcuate. On known parts of the upper dentition, *Ankylodon* differs from *Scenopagus* as follows: P^3 , much more transverse (buccolingually) and elongate (anteroposteriorly), with longer parastylar and metastylar salients, resembles a "T" instead of a triangle in occlusal outline, and is more nearly semimolariform. The paracone on P^3 is much larger and taller, the protocone is more prominent, and a small metacone is present. On P^4 , the lingual half of the crown is longer (anteroposteriorly), the protocone and paracone are taller, more spire-like, and the postmetacrista is higher and bears a tiny metacone. On M_{1-2} the hypocone and postcingulum are considerably enlarged, the lingual furrow between the hypocone and protocone is deeper and wider, the conules are larger, and the buccal edge of the crown is more emarginate. The metastylar salient is more expanded on M^1 , the parastylar area is greater on M^2 , and on M^3 the parastylar salient is greatly reduced relative to *Scenopagus*.

In effect, features that are diagnostic of *Scenopagus* are equally descriptive of *Ankylodon*, except for larger and higher, more nearly conical cusps, sharper, broader cingula, larger metastylar and parastylar salients on M^1 and M^2 , respectively, and greater anteroposterior compression of the trigonid on M_{1-3} . These differences between Bridgerian *Scenopagus* and Uintan-Chadronian *Ankylodon* may be a consequence of a continuation of similar trends in the same dental characters seen in the evolution of Wasatchian-Bridgerian species of *Scenopagus* from the Paleocene *McKennatherium*. Butler (1972) suggested, and I concur, that *Ankylodon* is the latest known adapisoricid. Comparison of *Ankylodon* with *Scenopagus* indicates that the ancestry of *Ankylodon* lies among the Bridgerian species of *Scenopagus*—a conclusion that Robinson and McKenna have also come to independently (McKenna, personal commun. 1975).

The lower dentition of *Ankylodon*, completely preserved on the AMNH "dark" specimen (Lillegraven and McKenna, MS), consists of three molars and seven antemolar teeth. As traditionally interpreted, the lower dental formula is $I_{2-3}C_1P_{1-4}M_{1-3}$. However, the homologies of the anterior teeth are un-

certain, and alternate interpretations of the lower antemolar dental formula are possible. Since the tips of both I_2 and I_3 are broken off, the identification of these teeth as incisors is tentative. I_2 is round and I_3 is oval in cross section. Both teeth are enlarged and project anterodorsally. I_3 , larger than I_2 , is concave along the posteromedial and posterolabial face of the crown, and bears a posterobasal cuspsule. Relative to I_2 , the morphology of I_3 may be interpreted as caniniform. The third tooth in the jaw—the alleged C_1 —is structurally identical to, and as premolariform as, the alleged P_1 , and as such, is the first of five premolariform teeth. These identifications can yield a lower antemolar dental formula of either $I_3C_1P_{1-5}$, or, if the two anterior lower teeth are incisors, $I_{2-3}P_{1-5}$. Some of the premolars may be retained deciduous teeth, as has been postulated for other preptotheres (McKenna, 1975). A fourth possible interpretation of homologies, which also pertains to the discussion below of the erinaceid *Litolestes ignotus*, concerns the identification of the third tooth in the jaw—the premolariform "canine." McDowell (1958: 157, Fig. 19A), has identified the deciduous C_1 in the insectivore *Nesophontes* as a premolariform, single-rooted tooth, which is very similar to the premolariform "canine" of *Ankylodon* (and *Litolestes ignotus*). However, calling this tooth dC_1 in *Ankylodon* (in an antemolar dental formula of $I_{2-3}dC_1P_{1-4}$) is premature, since the homology of this tooth locus in *Nesophontes* is perhaps also uncertain. The alleged permanent canine of *Nesophontes* is not caniniform, but, like its milk predecessor, is premolariform (McDowell, 1958: 157, Fig. 19C), and may represent a permanent premolar with a deciduous premolariform predecessor. The lower antemolar dental formula of *Ankylodon* is tentatively identified as: I_2, I_3 or $C_1, dP_1P_2P_3P_4P_5$. Clearly, until more complete material of the anterior dentition of *Ankylodon* and other adapisoricids is recovered, the homologies of the anterior teeth remain unsettled.

Macrocranium Weitzel, 1949

The genus *Entomolestes* was described by Matthew (1909) from the Middle Eocene Bridger Formation, with *E. grangeri* as the type species. Subsequently, Matthew (1918) named a second species, *Entomolestes nitens*, from the Early Eocene Willwood Formation. Since then, definite and tentative occurrences of *E. nitens* have been recorded from the Wasatch Formation, Colorado (McKenna, 1960a), the early Wasatchian Powder River local fauna, Wyoming (Delson, 1971), the Lysite and Lost Cabin Members, Wind

River Formation, Wyoming (Guthrie, 1967, 1971), the Wasatchian Almagre facies of the San Jose Formation, New Mexico (Robinson, 1968b), and Sparnacian-Cuisian localities in France (Russell, et al., 1975). No additional material referable to *E. grangeri* has been recovered since its original description.

Robinson (1968b) and Butler (1972) suggested that *E. nitens* was generically distinct from *E. grangeri* and should be referred to *Scenopagus*. Guthrie (1971) disagreed, citing differences between *E. nitens* and *Scenopagus* in the structure of the upper molars, and retained the use of *E. nitens*.

From examination of the type, paratype, and a large amount of material referred to *E. nitens*, it is clear that Robinson (1968b) and Butler (1972) were correct in observing the generic disparity between *E. grangeri* and *E. nitens*. Perhaps the affinities of the former, as discussed in a later section, are with the Erinaceidae. Although P_4 in both species is similarly premolariform, the talonid is much shorter on that of *E. grangeri*. M_{1-3} of *E. grangeri* have less robust cusps, comparatively shorter talonids with more nearly straight posterior margins, more triangular trigonids, reduced hypoconulids, and shallower talonid basins, compared to *E. nitens*.

As described below, *E. nitens* is also distinct from *Scenopagus*, but is virtually identical to *Macrocranium tenerum* (= *Messelina*) hitherto known only from the middle Eocene of Europe. *Macrocranium* was shown by Tobien (1962) to be a senior synonym of *Aculeodens* and was referred to the Amphilemuridae of McKenna (1960a), although Van Valen (1967) considered the genus to be a creotarsine adapisoricid. *Messelina tenera* (Tobien, 1962) was recently, and I think correctly, referred to *Macrocranium* (as *M. tenerum*) by Russell, et al. (1975). These authors have also commented on the remarkable similarity between *E. nitens* and *Macrocranium*, especially in the lower dentition. Except for the occurrence of a posterior cingulid on M_{1-2} of *M. tenerum*, distinction between that species and *E. nitens* is difficult. Nonetheless, Russell, et al. (1975), claimed that the presence of a tiny metacone on P^4 of *E. nitens* from Four Mile, as well as the greater transverse nature of M_{1-3} compared to *Macrocranium* warranted generic separation of the two species. But, as described below, P^4 of *E. nitens* from the Almagre does not possess a metacone. Although I have not examined the original material of upper molars of *Entomolestes* cf. *nitens* from Europe (Russell, et al., 1975), the illustrations imply that part of the hypodigm (notably, Mu-118-L, Av-841-Bn) may be referable to

Scenopagus, upper molars of which are indeed more transverse than those of *E. nitens*. M^1 of *M. tenerum* as figured in Tobien (1962) is similar in crown proportion to that of *E. nitens*. The reconstruction and figures of M_{2-3} of *M. tenerum* are apparently inaccurate (Russell, et al., 1975). *E. nitens* and *E. cf. nitens* from the early Eocene of North America and Europe are here considered species of *Macrocranium*.

Macrocranium nitens

(Matthew, 1918), new combination

(Fig. 7; Tables 4, 5)

TYPE: AMNH 15697, partial right mandible with P_4 - M_2 from the Willwood Formation, Big Horn Basin, Wyoming.

PARATYPE: AMNH 14674, partial right mandible with $\frac{1}{2}$ P_4 - M_3 from the Lysite Member, Wind River Formation, Wyoming.

REFERRED SPECIMENS: AMNH 48187, RM_3 ; AMNH 48174, RP_4 - M_3 ; AMNH 48188, frag. P_4 ; AMNH 48179, RP_4 - M_2 ; AMNH 48189, LP_4 - M_2 ; AMNH 48181, frag. talonid; AMNH 48176, LP_4 - M_3 ; AMNH 48182, RM_2 ; AMNH 48172, LM_{2-3} ; AMNH 48178, LP_4 - M_3 ; AMNH 48180, RP_4 - M_2 ; AMNH 48184, RM_{1-2} ; AMNH 48177, LP_4 - M_2 ; AMNH 48175, RM_{1-2} ; TTU-P-4211, RP_4 - M_2 ; CM 12398, LM_{1-3} ; CM 22019, RM_2 ; CM 22014, LM_{2-3} .

LOCALITIES: Quarry 88, Almagre facies, San Jose Formation, New Mexico; Lysite and Lost Cabin Members, Wind River Formation, Wyoming; Willwood Formation, Big Horn Basin near Otto, Wyoming.

KNOWN DISTRIBUTION: Wasatchian, New Mexico, Wyoming.

DESCRIPTION: The description presented here is based on the holotype, the paratype, and the single quarry sample from the Almagre. Teeth anterior to P_3 and P^4 are unknown. P_3 is a single-rooted, very small, peg-like tooth, with one laterally compressed, anterior-leaning cusp.

P_4 is variable in structure, more so than the lower molars, and more than has been noted in previous descriptions. It is a large, two-rooted premolariform tooth with a three-cusped trigonid and lower, shorter, talonid. The protoconid is large and robust, leans posteriorly, and occupies most of the basal area of the trigonid. The paraconid is low, conical, and arises from the anterolingual part of the base of the protoconid. The two cusps are continuous labially, but are demarcated lingually by a weak vertical groove. A paracristid extends down the anterior face of the protoconid to the paraconid, joining the two cusps along the entire height of the paraconid. The metaconid, slightly higher than the paraconid, but only one-third the height of the protoconid, occurs low on the posterolingual face of the protoconid, and varies in size from a small bulge (on the holotype AMNH 15697) to a conical cusp (on the Almagre

specimens). In the latter condition a V-shaped notch separates the metaconid and protoconid.

The structure of the talonid of P_4 is most variable. On all specimens examined, the talonid is low, as wide as, or wider than, the trigonid basally, and approximately one-half as long. An extremely weak cristid obliqua extends directly posteriorly from the trigonid to a raised point (?hypoconid) on the posterior rim of the talonid, and delimits the labial margin of a shallow talonid basin. The width of the basin from the lingual margin of the talonid to the cristid obliqua represents only the lingual one-third of the total basal width of the talonid. A hypoflexid groove for occlusion of the paracone of P_4 slopes very gently labioventrally from the cristid obliqua to the basal margin of the talonid. Since the cristid obliqua is very weak, it is almost obscured by wear on many of the specimens. On some of the material from the Almagre, an additional cuspule occurs on the raised posterior rim of the talonid basin in the position of an entoconid. A precingulum, when present, is weak and short. These variations seem taxonomically insignificant, and in each case, the P_4 is associated in a partial mandible with molars of *M. nitens*.

The molars of *M. nitens* are large, robust teeth that lean lingually, and are almost rectangular in occlusal outline. The talonid is longer and only slightly lower than the trigonid on M_{1-3} , and wider than the trigonid on M_{1-2} . A slight lateral constriction occurs basally between the trigonid and talonid. The protoconid and metaconid are low, conical, almost bulbous cusps, with the metaconid slightly larger and taller. A strong, broad paracristid runs anterolingually from the anterior face of the protoconid, and terminates well anterior to the metaconid, so that the trigonid is open lingually. The paraconid is a barely discernible bulge, anteroposteriorly compressed at the lingual end of the paracristid.

The talonid on M_{1-3} bears a large, rounded entoconid, almost as tall as the metaconid, and a much lower hypoconid that becomes flat with wear. On M_{1-2} , the hypoconulid is low, small, and occurs slightly lingual to the midline on the same wall as the entoconid. On M_3 the hypoconulid is medial, distinct, as large as the entoconid, and projects posterodorsally. The cristid obliqua is long, broad, and strong, and originates directly below the notch between the protoconid and metaconid. The hypoflexid notch is shallow, the precingulid is very weak, and a postcingulid does not occur. Characteristically, on M_1 the labial part of the base of the trigonid bulges anterolabially and the

paracristid is sharply angled at the anterior part of the base of the protoconid. This lends the M_1 trigonid a very squared appearance in occlusal view, relative to the more nearly triangular trigonid on M_{2-3} . Similarly, the base of the talonid below the hypoconid on M_{1-2} is expanded labially and posteriorly.

Upper dentitions of *M. nitens*, although noted from Lost Cabin (Guthrie, 1971) and from the Almagre (Robinson, 1968b), have never been adequately described. Two specimens, AMNH 48177 and AMNH 48175, comprising P_4+M^3 and M^{1-2} respectively, occur in the single quarry sample of *M. nitens* from the Almagre.

Only the labial half of P_4 is preserved on AMNH 48177. The broken crown bears a very large, tall, and conical paracone, a small anterolabial parastyle, and a short posterolabial metastylar salient. The paracone is approximately twice as high and large as that on M^{1-2} . There is no evidence of a metacone on P_4 , although a weak crest runs vertically along the posterior face of the paracone to the tip of the metastylar salient. The buccal margin of the crown is shallowly convex labially.

M^{1-2} , essentially rectangular in occlusal outline, are not transverse and are only weakly constricted anteroposteriorly across the conules. The buccal borders of the crowns are shallowly emarginate and the lingual margins are oriented posterolingually. The parastylar and metastylar areas are small and not expanded, although the parastylar salient on M^1 juts anteriorly beyond the remaining anterior margin of the crown. The paracone and metacone, low, subequal, conical cusps, are well separated and occur close to the labial border of the crown, leaving virtually no stylar area. The protocone is low, pyramidal, only slightly compressed anteroposteriorly, and forms the anterolingual corner of the crown. The hypocone, rounded and conical, is only slightly lower than, but almost as large as, the protocone, and forms the posterolingual corner of the crown. A shallow lingual valley between the protocone and hypocone divides the lingual length of the crown into approximately equal halves. A weak crista extends anterolabially from the hypocone to the anterior wall of the trigon below the preprotocrista. The conules are low, but well developed, conical and subequal, and are linked to the protocone by strong protocristae. The preparaconulecrista and postmetaconulecrista are weakly developed, but extend to the parastyle and metastyle, respectively, and delineate a narrow paracingulum and metacingulum. The postmetacrista is weak, low, and not crest-like. A short narrow precingulum occurs on M^{1-2} .

M³, triangular in occlusal aspect, has a greatly reduced metastylar area and a relatively tiny metacone, approximately two-thirds the size of that of M². The paracone and parastylar salient are unreduced relative to M². M³ lacks a hypocone, and the postcingulum is very short.

REMARKS: *Macrocranion nitens* and *Scenopagus* are easily distinguished in known parts of the dentition, although P₄ and the upper molars are similar in both forms. In contrast to *Scenopagus*, the metaconid on P₄ of *M. nitens* is more nearly separate from the protoconid, the cristid obliqua is considerably weaker, the posterolabial part of the base of the talonid is expanded, the posterior rim of the talonid basin is raised, and the slope of the hypoflexid groove is lower.

Compared to *Scenopagus*, M₁₋₃ of *M. nitens* are lower, their bases are fattened labially (exodaenodonty), the trigonid is much lower relative to the talonid, the talonid is proportionately wider and considerably longer than the trigonid, and the cusps are lower and more bulbous. In *M. nitens*, the paraconid is better developed, more anterior and not as close to the metaconid, the trigonid on M₁ is open lingually and more nearly square in occlusal outline, the hypoconid is less compressed anteroposteriorly, the cristid obliqua is longer and meets the trigonid more lingually, and the precingulid is weaker.

P₄ of *M. nitens* differs from *Scenopagus* in having a convex labial margin, very small stylar salients, and a much weaker, lower paracone-metastylar crest. The upper molars of *M. nitens* are less transverse, more nearly rectangular in occlusal outline, and less constricted across the conules. The labial margins of the molars are less emarginate, the stylar areas are much smaller and not expanded, and the cusps are lower and more nearly conical. In *M. nitens*, the hypocone is higher relative to the protocone and occupies more of the lingual area of the crown, the postmetacrista is much weaker and less crest-like, and the metacingulum is narrower.

Macrocranion cf. *M. nitens*
(Fig. 8; Tables 4, 5)

REFERRED SPECIMENS: AMNH 59673, LP₄-M₃; AMNH 59662, RP₄; AMNH 59656, RM₂₋₃; AMNH 59663, RP₄; AMNH 80071, RM₁; AMNH 59679, RP₄-M₁; AMNH 59651, RP₄; AMNH 59688, LP₃₋₄; AMNH 88846, LM₁; AMNH 88834, RM₁; AMNH 88839, LM₁; AMNH 88830, LM₁₋₂; AMNH 56318, RP₃₋₄; AMNH 59678, RP₄-M₂; AMNH 88837, LM₁.

LOCALITIES: E. Alheit, Despair and Kent Quarries, Four Mile local fauna, Hiawatha Member, Wasatch Formation, Colorado; Powder River local fauna, Bozeman locality, Wyoming.

KNOWN DISTRIBUTION: Early Wasatchian, Colorado and Wyoming; Sparnacian and Cuisian, France.

DESCRIPTION AND REMARKS: McKenna (1960a) and Delson (1971) noted the occurrence of a species of *Entomolestes* cf. *E. nitens* in the Four Mile and Powder River faunas, respectively, which was 20% smaller than the type and paratype of *E. nitens*. Although the Almagre sample of *M. nitens* increases the known variation in size of the species, the original and additional material from Four Mile is here referred to *Macrocranion* cf. *M. nitens*. This species is virtually identical to *M. nitens* in the morphology of the known parts of the dentition. The greatest difference in size occurs in the P₄, especially in the talonid. Recovery of a sizeable sample of *M. nitens* from early Wasatchian horizons should resolve the specific status of the Four Mile and Powder River material. Although the two specimens of upper dentition from Four Mile (AMNH 59678, 88837) agree in size with *M. nitens* from the Almagre, these are tentatively referred to cf. *M. nitens* on the basis of the morphology of P₄. P₄ on AMNH 59678 bears a well-developed paracone, a paracone-metastylar crest and a wear facet on this crest, where a tiny metacone occurred. This is similar to the condition on UCMP 44085 from Four Mile, which was described and figured (McKenna, 1960a) as *Entomolestes* cf. *E. nitens*. P₄ of *M. nitens* from the younger Almagre deposits lacks a metacone. Larger samples of *M. nitens* and cf. *M. nitens* may prove the presence of a tiny metacone on P₄ to be variable. If not, however, the implied loss of the metacone on P₄ during the Wasatchian in *M. nitens* would be consonant with the general trend of premolarization of P₄ in early Tertiary erinaceomorphs.

The isolated teeth from the Sparnacian and Cuisian of France, which Russell, et al. (1975) described as *Entomolestes* cf. *nitens*, exhibit an inordinate range of variation in size. Their structure is virtually identical to *Macrocranion nitens* and *M. cf. M. nitens* from North America, including the occurrence of exodaenodonty along the labial margin of M₁₋₂. It seems probable that the two species of *Macrocranion* recorded here are also represented by the material from the early Eocene of France.

Talpavus Marsh, 1872

This genus has also had a checkered history. *T. nitidus* was named by Marsh (1872) on the basis of two jaw fragments, one with 1/2M₁-M₂, and the other with a single premolar. The latter proved to belong to *Peratherium*, a marsupial (Robinson 1968b), whereas

**7
A****7
B****7C****8**

Table 4. Dimensions of lower teeth of *Macrocranium nitens* and *Macrocranium* cf. *M. nitens*

	P ₄		L	M ₁		L	M ₂		L	M ₃	
	L	W		AW	PW		AW	PW		AW	PW
<i>M. nitens</i>	1.6- 2.0	1.1- 1.3	1.9- 2.1	1.3- 1.5	1.5- 1.6	1.8- 2.1	1.4- 1.6	1.5- 1.7	1.9- 2.2	1.2- 1.4	1.3- 1.4
Mean	1.77	1.20	1.94	1.43	1.54	1.96	1.49	1.60	2.06	1.30	1.35
N.	6	7	9	8	9	11	10	10	5	5	5
SD.						0.09	0.07	0.04			
CV.						4.84	5.00	2.94			
<i>Macrocranium</i> cf. <i>M. nitens</i>	1.4- 1.7	0.9- 1.1	1.6- 1.8	1.3- 1.4	1.4- 1.5	1.7- 1.8	1.4- 1.5	1.5- 1.6	1.7	1.2	1.3
Mean	1.47	0.97	1.76	1.36	1.47	1.73	1.43	1.53			
N.	6	6	7	7	7	3	3	3	2	1	2

Table 5. Dimensions of upper teeth of *Macrocranium nitens* and *Macrocranium* cf. *M. nitens*

	p ₄		M ¹		M ²		M ³	
	L	W	L	W	L	W	L	W
<i>M. nitens</i>								
AMNH 48175			—	2.5	1.8	2.5		
AMNH 48177	1.8	—	1.8	2.5	1.7	2.7	—	—
CM 12398			2.0	2.6	1.7	2.5	1.3	1.8
CM 22019					1.9	2.5		
Mean			1.90	2.53	1.78	2.55		
<i>Macrocranium</i> cf. <i>M. nitens</i>								
AMNH 59678	—	2.2+	1.9	2.3	1.8	2.5		
AMNH 88837			1.9	2.3				

◀ Fig. 7. *Macrocranium nitens*. (A) Type, AMNH 15697, RP₄-M₂, Willwood Formation, Wyoming, approx. X 12; (B) AMNH 48178, LP₄-M₃, San Jose Formation, New Mexico, approx. X 12; (C) AMNH 48177, LP₄-M₃, San Jose Formation, New Mexico, approx. X 16.
Fig. 8. *Macrocranium* cf. *M. nitens*, AMNH 59673, LP₄-M₃, Wasatch Formation, Colorado, approx. X 12.

the former, YPM 13511, was referred by Matthew (1909) to *Nyctitherium*. After *T. nitidus*, based on YPM 13511, was re-established as distinct from *Nyctitherium* (McKenna, et al., 1962), only four additional specimens were referred to that genus: AMNH 55686, a partial lower jaw with M_3 of *Diacodon bacchanalis* from the late Bridgerian "Hyopsodus" Hill locality; CM 12061, partial lower jaw with P_4 - M_3 from Myton Pocket, Uintan of Utah (McKenna, et al., 1962); AMNH 55662, partial lower jaw with P_4 - M_3 from the Huerfano local fauna, late Wasatchian of Colorado (Robinson, 1966); and YPM 16334, partial lower jaw with P_4 - M_2 from the upper part of the Bridger Formation, Wyoming (Robinson, 1968b).

A second species of *Talpavus*, *T. sullivanii*, was described by Guthrie (1967; 1971) from the Lysite and Lost Cabin Members of the Wind River Formation, Wyoming. A number of the teeth referred to this species are here identified as *Scenopagus*. The remaining portion of the hypodigm is distinct from *Talpavus* and needs restudy. Robinson (1968b) also referred the Paleocene *Leipsanolestes seigfriedti* Simpson, 1928, to *Talpavus* although that species had previously been allied with *Entomolestes* (McKenna, 1960a). *Leipsanolestes* is distinct from both *Talpavus* and *Entomolestes* and is discussed in a later section.

The confusion and distinction between the allegedly similar *T. nitidus* and *Entomolestes grangeri* were dealt with by Robinson (1968b). Delson (1971) recognized Robinson's criteria, but inexplicably synonymized the species of *Scenopagus* with *Talpavus*.

The major problem in defining *Talpavus* is the fragmentary nature of the type specimen, YPM 13511, and the resulting paucity of diagnostic criteria. However, four features on the type appear to me to be distinctive and indicative of its affinities: the paraconid, preserved only on M_2 , is compressed anteroposteriorly into a thin, high crest that flares anterolaterally at its lingual end; the entoconid is much higher than the hypoconid; the talonid and trigonid are of equal width; the hypoconulid, small and slightly lingual in position, occurs at the posterolabial part of the base of the entoconid and is delineated from that cusp by a sharp notch. The juncture of the hypoconulid and hypoconid is not as well marked, and with wear, the two cusps are joined by a hypocristid. The first two characters align the type of *T. nitidus* with adapisoricids; the latter ones distinguish it from

Scenopagus priscus, the adapisoricid most similar in size and structure to *T. nitidus*. On M_2 of *S. priscus* the talonid is narrower than the trigonid, the hypoconulid is larger and more clearly separate from the hypoconid, and the paraconid is formed as a broader, flatter lophid.

Talpavus nitidus Marsh, 1872

(Fig. 9; Table 6)

REFERRED SPECIMENS: YPM 16334, LP_4 - M_2 ; CM 13717, LP_4 - M_2 ; AMNH 11488, LM_{2-3} ; AMNH 55686, RM_3 .

LOCALITIES: Dry Creek, Henry's Fork, and locality 5, Bridger Formation (Upper), Wyoming; Powder Wash, Green River Formation, Utah.

KNOWN DISTRIBUTION: Bridgerian, Wyoming, Utah.

REMARKS: I concur with Robinson's (1968b) description of *T. nitidus*, which was based on the type and YPM 16334. The latter specimen and the other material referred here resemble the type, and differ from *S. priscus* in those features noted above: the paraconid on M_2 is thinner, more blade-like, the talonid is as wide as the trigonid, and the hypoconulid is smaller and not as clearly separated from the hypoconid. Apart from the structure of M_2 , examination of the referred material of *T. nitidus* discloses additional diagnostic criteria, especially a narrow, premolariform P_4 with an unbasined talonid. Significantly, the talonid of P_4 also lacks cusps—a major distinction between *T. nitidus* and other material ascribed below to *Talpavus*. The structure of P_4 , the paraconid on M_1 , and the triangular, uncompressed trigonid on M_1 also distinguish *T. nitidus* from *S. priscus*. In *S. priscus*, P_4 is wider, the talonid is basined, the metaconid is less well developed, the trigonid on M_1 is more nearly square in occlusal outline, and the M_1 paraconid is a stronger lophid, more nearly vertical, and closer to the metaconid.

Talpavus cf. *T. nitidus*

(Fig. 10; Table 6)

REFERRED SPECIMENS: CM 12122, LP_4 - M_3 ; CM 13715, RP_{3-4} ; CM 13716, LP_4 - M_1 ; CM 13718, RP_{3-4} , CM 13754, RM_1 ; CM 26087, LP_3 - M_1 ; CM 26260, LM_{1-3} ; CM 26261, RM_{1-2} ; CM 31180, LP_3 - M_3 ; CM 31181, RM_3 ; CM 26267, RP_4 - M_3 ; AMNH 55226, LP_4 - M_3 .

LOCALITIES: Greybull horizon, Willwood Formation, Big Horn Basin, Wyoming; Powder Wash, Green River Formation, Utah; Huerfano Formation, Colorado.

KNOWN DISTRIBUTION: Early Wasatchian, Wyoming; early Bridgerian, Utah; late Wasatchian, Colorado.

Fig. 9. *Talpavus nitidus*, CM 13717, RP_4 - M_2 , Green River Formation, Utah, approx. X 20. Fig. 10. *Talpavus* cf. *T. nitidus*. (A) CM 12122, LP_4 - M_3 , and (B) CM 26260, LM_{1-3} , Willwood Formation, Wyoming, approx. X 12; (C) CM 26087, LP_3 - M_1 , Green River Formation, Utah, approx. X 12. Fig. 11. *Talpavus duplus*, new species. Type, CM 12061, LP_4 - M_3 , Uinta Formation, Utah, approx. X 12.



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REMARKS: Only two features distinguish this material from *T. nitidus*: slightly smaller size and the occurrence of two cuspsules (?entoconid and hypoconulid) on the raised posterior margin of the talonid of P_4 . P_3 , preserved on CM 13715, CM 13718, CM 26087, and CM 31180, is smaller than P_4 , double-rooted, somewhat laterally compressed, and bears a small paraconid, a protoconid and a short talonid. As in *T. nitidus*, P_4 of cf. *T. nitidus* is narrow, and its talonid is short, unbasined, and lacks a cristid obliqua. The P_4 metaconid is almost as large and tall as the protoconid, and the paraconid is low, rounded, and well developed. The trigonid on M_1 is not compressed, but triangular in occlusal aspect, and the paraconid is blade-like and canted anterolingually, so that the trigonid is open lingually. The trigonid on M_2 is more compressed than on M_1 , and is as wide as the talonid. The hypoconulid on M_{1-2} is slightly more separated from the hypoconid in comparison to the condition in *T. nitidus*, but is smaller than in *S. priscus*. The occurrence of cuspsules on the talonid of P_4 may prove variable with recovery of additional *Talpavus* material. The structure of the known parts of the dentition of *Talpavus* implies that *Talpavus* had an origin in common with *Scenopagus*, especially *S. priscus*, from a *McKennatherium*-like adapisoricid, and differentiated with respect to the loss of the talonid basin on P_4 .

AMNH 55226 from Huerfano was referred by Robinson (1966) to *Talpavus* cf. *T. nitidus*—an action recently questioned by Russell, et al. (1975) in their confusing analysis of *Talpavus*. Although wear on P_4 of AMNH 55226 has obliterated the details of the talonid structure, the latter appears to have been unbasined. Similarly, breakage and subsequent repair of the trigonids on M_{1-2} have produced artificially elongate molars. Nevertheless, as in *Talpavus*, the M_2 talonid is as wide as the trigonid, the hypoconulid on M_{1-2} is smaller than in *S. priscus* and is joined by a hypocristid to the hypoconid, P_4 is much narrower in relation to M_1 than is the case in *S. priscus*, and the paraconid on M_2 flares anterolingually.

Talpavus duplus, new species (Fig. 11; Table 6)

TYPE: CM 12061, RP_4 - M_3 , and only known specimen.

TYPE LOCALITY: Myton pocket, Uinta Formation, Utah.

KNOWN DISTRIBUTION: Uintan of Utah.

ETYMOLOGY: *duplus*, L., double, referring to the double paraconid on P_4 and the close resemblance to *T. nitidus*.

DIAGNOSIS: Largest known species of *Talpavus*. Two cuspsules form the paraconid on P_4 .

DESCRIPTION AND REMARKS: The features that define *Talpavus* are well expressed on CM 12061. On P_4 the talonid is unbasined, but bears two cuspsules in a fashion similar to P_4 of *Talpavus* cf. *T. nitidus*. The metaconid on P_4 is almost as large as the protoconid. The paraconid is formed as a ridge running antero-lingually from the anterior face of the protoconid. Two cuspsules occur on the ridge, one proximal to the protoconid and one forming the tip of the paraconid.

Apart from their larger size, M_{1-3} of *T. duplus* are similar to those of *T. nitidus* and cf. *T. nitidus*. The paraconid on M_1 , although worn, appears to have been closer to the metaconid than in the latter species. However, features of *T. duplus* that are typical of *Talpavus* are the uncompressed trigonid on M_1 , M_2 talonid and trigonid of equal width, and the small hypoconulid joined to the hypoconid by a hypocristid on M_{1-2} . *T. duplus* appears to be a Uintan representative of the same lineage that gave rise to the Wasatchian-Bridgerian species of *Talpavus*.

Adapisoricidae: Summary

The five genera, *McKennatherium*, *Scenopagus*, *Ankyledon*, *Macrocranion*, and *Talpavus*, seem to comprise a clade of lipotyphlans distinct from other early Tertiary Erinaceomorpha and Soricomorpha. The major trends in the origin and radiation of Paleocene and Eocene Adapisoricidae appear to be premolarization of the fourth premolar and the development of more nearly rectangular molars with lower, more bunodont cusps—trends shared with early erinaceids and many other early Tertiary mammals. In general, these are adaptations that emphasize crushing rather than puncturing and shearing during mastication. Specifically, P_4 in adapisoricids is primitively semimolariform, but becomes premolariform in Eocene species. M_{1-3} are characterized by a compressed, lophid-like paraconid that never joins the metaconid. The protoconid and metaconid are low, conical, almost bulbous cusps. The talonid is wide, moderately basined, and bears a high entoconid and a lower hypoconid that flattens with wear. The hypoconulid is median or barely lingual in position, and is not reduced. The hypoflexid notch is shallow; i. e., the cristid obliqua meets the trigonid below and labial to the notch between the protoconid and metaconid. Labial, lingual, or posterior cingulids are not developed.

The cusps on the upper molars are relatively low and conical. The styler shelf is very narrow, without styler cusps, and the hypocone and conules are well developed. In occlusal view, M^{1-3} are essentially rec-

tangular and somewhat or moderately transverse. P₄, as yet unknown in Paleocene species, is premolariform in Eocene adapisoricids.

North American Paleocene adapisoricids are represented by *McKennatherium ladae* and a larger, contemporaneous species from the Rock Bench Quarries, Polecat Bench Formation. The Eocene genus *Scenopagus*, including *S. edenensis*, *S. curticens*, and *S. priscus*, seems descended from *McKennatherium*, and ancestral to the late Eocene and Oligocene *Ankylodon*, the youngest known genus of the Adapisoricidae. *Talpavus*, represented by at least two species during the Eocene, has lost the talonid basin on P₄. *Macrocranium* may have had a European origin, but one species, *M. nitens*, occurs in early Eocene deposits of western North America. There is ample evidence that extensive faunal interchange occurred between North America and Europe during the Paleocene and early Eocene across a North Atlantic land corridor (Savage, 1971; Szalay and McKenna, 1971; McKenna, 1971, 1972a, 1972b; Dawson, et al., in press).

The bulk of recent work concerning early Tertiary

lipotyphlans alludes to an ancestral-descendant relationship between adapisoricids and erinaceids, an inference that may have seemed possible if the Adapisoricidae were defined in a wastebasket sense (Van Valen, 1967, for example). As here understood, however, the two groups, by mid-Paleocene time, had differentiated to an extent that implies a considerable period of independent evolution prior to their earliest known (and contemporaneous) occurrence. Knowledge of their ancestry is clouded and will probably remain so until the record of North American Cretaceous eutherians improves, and until a number of early Paleocene faunas, which are currently under investigation, are described. Clemens (1973) has examined and tentatively refuted the possible relationships between *McKennatherium* and the late Cretaceous leptictid *Gypsonictops*. It also seems unlikely that adapisoricids originated from Late Cretaceous palaeoryctids, e. g., *Cimolestes*, *Procerberus*, or *Batodon*, for reasons similar to those stated by Clemens (1974) concerning the ancestry of the paromomyid primate *Purgatorius*. Palaeoryctid lower dentitions are characterized by tall

Table 6. Dimensions of lower teeth of *Talpavus nitidus*, *Talpavus* cf. *T. nitidus*, and *T. duplus*, new species

	P ₄			M ₁			M ₂			M ₃	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>T. nitidus</i>											
YPM 13511			---	---	1.2	1.6	1.1	1.1			
CM 13717	1.1	0.8	1.4	1.1	1.1	1.4	1.2	---			
AMNH 11488						1.4	1.2	1.2	1.3	1.0	0.8
<i>Talpavus</i> cf. <i>T. nitidus</i>											
CM 12122	1.1	0.7	---	---	---	1.2	---	1.0	1.1	---	---
CM 13715	1.2	0.8									
CM 13716	1.2	0.7	1.4	---	1.1						
CM 13718	1.1	0.8									
CM 13754			1.5	1.0	1.1						
CM 26087	1.1	0.7	1.4	1.0	1.0						
CM 26260			1.3	1.1	1.0	1.1	1.0	1.0	1.2	0.9	0.6
CM 26261			---	1.1	1.2	1.2	1.1	1.1			
CM 31180	1.1	0.8	1.3	1.0	1.0	1.1	1.0	1.0	1.2	0.9	0.7
CM 31181									1.2	0.9	0.8
CM 26267	1.0	0.7	1.4	1.1	1.0	1.2	0.9	0.9	1.2	0.9	0.7
AMNH 55226	1.2	0.8	1.4	1.1	1.1	1.4	1.1	1.1	1.4	1.0	0.7
Mean	1.12	0.75	1.38	1.05	1.06	1.20	1.02	1.02	1.24	0.92	0.70
<i>T. duplus</i>											
CM 12061 Type	1.4	0.9	1.6	1.1	1.2	1.6	1.2	1.2	1.6	1.1	1.0

trigonids and high, sharp cristids and cusps. Their upper molars are very transverse and lack hypocones or posterior cingula—features contrary to the more bunodont dental adaptations of adapisoricids. Some of the material of *Purgatorius* from the Puercan Garbani Locality, Montana, is, according to Clemens (1974), of definite insectivoran aspect, and in my view, especially like *McKennatherium*. The late Cretaceous erinaceotan from Alberta (Fox, 1970) seems to be a representative of a non-paleoryctid—leptictid group of insectivores that may have been ancestral to adapisoricids—a suggestion that Clemens (1974) also makes with reference to the ancestry of *Purgatorius*. In terms of dental morphology, the same Cretaceous stock that gave rise to adapisoricids (and other Lipotyphla) was probably also basal to the radiation of primates, dermopterans, bats, and tupaiids (the Archonta of Gregory, 1910, minus macroscelidids) as well as ungulates (McKenna, 1975).

Family Erinaceidae Fischer Von Waldheim, 1817

Many of the known early Tertiary insectivores have at one time or another been referred to this family. Simpson's (1945) Erinaceidae included *Entomolestes*, *Proterixoides*, *Metacodon*, and *Ankylodon*. Subsequently, *Scenopagus*, *Centetodon*, and *Talpavus* were also placed here (McKenna and Simpson, 1959; McKenna et al., 1962; Robinson, 1966). Van Valen (1967) limited the Erinaceidae to undoubted post-Eocene forms and relegated the above genera to the Adapisoricidae. These are now more strictly defined in this and other studies.

The early Tertiary North American Erinaceidae, as here understood, includes *Litolestes*, *Leipsanolestes*, possibly *Entomolestes grangeri*, and an unpublished form from the late Eocene of Wyoming (Setoguchi, M. S. thesis; McKenna, personal commun., 1974). Their shared-derived characters include a premolariform P₄, rectangular molars that progressively decrease in size from M₁₋₃, a dorsally flattened but cusped paraconid on M₂₋₃, a greatly reduced hypoconulid, and a V-shaped talonid basin.

I agree with Butler (personal commun., 1975) and Russell (1964) that the European Paleocene *Adapisorex* is an erinaceid rather than an adapisoricid.

Litolestes Jepsen, 1930

L. ignotus, from the late Tiffanian of Wyoming, was described by Jepsen (1930) from partial remains of the lower dentition, and was referred, with question, to the Insectivora. In subsequent descriptions of two

additional species, *L. notissimus* (Simpson, 1936) from Scarritt Quarry and *L. lacunatus* (Gazin, 1956) from Bison Basin, *Litolestes* was identified as a hyopodontid condylarth. Van Valen (1967) however, returned *Litolestes* to the Insectivora as a creotarsine adapisoricid.

Although *Litolestes* is here described as an erinaceid, the affinities of *L. notissimus* and *L. lacunatus* are not as clear. As discussed below, they do not resemble typical hyopodontids. Rather, they may represent late Paleocene echinosoricine-like erinaceids.

Litolestes ignotus Jepsen, 1930

(Fig. 12; Table 7)

TYPE: PU 13362, RP₄-M₃, Polecat Bench Formation, Wyoming.

REFERRED SPECIMENS: PU 13354, LP₄-M₂; PU 13974, RP₄-M₃; PU 14064, RP₃-M₂ erupting; PU 19362, LP₃-M₃; PU 19387, LP₂-M₂.

LOCALITY: Silver Coulee Quarries, Polecat Bench Formation, Wyoming.

KNOWN DISTRIBUTION: Late Tiffanian, Wyoming.

DESCRIPTION AND REMARKS: The lower antemolar dentition of *L. ignotus* has been dealt with elsewhere (Schwartz and Krishtalka, 1976) and need not be redescribed in detail. I₂₋₃ of *L. ignotus* are comb-like with digitate, trilobed crowns. The crowns on lower incisors of later Tertiary and Recent erinaceids are not divided, but spatulate. However, incisors with divided crowns are not characters that imply phyletic relationships, inasmuch as these have evolved independently in many groups of mammals including Dermoptera, Macroscelidea, Carnivora, Notoungulata, and a variety of living and extinct insectivores (cf. Rose, 1973).

The fourth tooth in the jaw, traditionally identified as the canine in *L. ignotus*, is small, single-rooted, and fully premolariform. On this and other bases, Schwartz and Krishtalka (1976) concluded that this tooth may represent the first of five lower premolars in *L. ignotus* (and in the dermopteran *Plagiomene multicuspis*). As noted previously concerning *Ankylodon*, in addition to identifying this tooth as a premolariform canine or a premolar, a third interpretation—a deciduous canine—is possible, since the alleged dC₁ in another insectivore, *Nesophontes*, is also small, single-rooted, and premolariform. However, the homology of that locus in *Nesophontes* is uncertain, since both “dC₁” and “C₁” are premolariform and perhaps represent a deciduous premolar and its permanent successor, respectively. Accordingly, the tooth immediately posterior to I₃ in *L. ignotus* (and *Plagiomene*) is here tentatively identified as dP₁, a premolariform deciduous premolar that

is retained in an antemolar dental complement of $I_1I_2I_3dP_1P_2P_3P_4P_5$. However, in the following portion of this paper, the standard post-incisor nomenclature of C_1P_{1-4} is employed for reasons outlined in the introduction and to facilitate comparisons of canine and premolar morphologies.

P_4 is premolariform and as large as M_1 , as in typical early erinaceomorphs. The protoconid is dominant, the paraconid is small and anterolingual, and the metaconid is low on the posterolingual slope of the protoconid. The talonid is short, as wide as or wider than the trigonid, and the talonid basin is lingual and very narrow—approximately one-fourth or one-fifth of the width of the talonid. A tiny cuspule occurs at the posterior tip of the cristid obliqua. The labial portion of the talonid slopes ventrolabially away from the cristid obliqua.

The molars decrease markedly in size from M_1 to M_3 . The protoconid and metaconid are low and conical. Significantly, the paraconid on M_1 is slightly compressed, but is more nearly erect and cusped than on M_{2-3} . On the latter, the paraconid is more nearly medial and flattened so that it projects anteriorly. The talonid is as long and wide as the trigonid on M_{1-2} , but is elongate on M_3 because of a posteriorly projecting hypoconulid. The entoconid is higher than the hypoconid, but neither cusp is formed as a distinct cone. Rather, they are elongate anteroposteriorly, with flat internal walls that slope ventromedially so that the talonid basin is not rounded, but a V-shaped valley. The internal walls of both cusps extend to the trigonid and close the talonid basin lingually and labially. The bottom of the talonid valley is formed as a midline, which runs from the trigonid to the posterior margin of the talonid. On M_{1-2} the hypoconulid is extremely reduced and occurs on the posterior edge of the entoconid wall, just lingual to the midline. The posterior edge of the talonid is nearly straight.

These features of *L. ignotus* are equally diagnostic of undoubted later Tertiary erinaceids and, most especially, a new mid- or late-Eocene species from the Tepee Trail Formation, Wyoming, currently being described by McKenna (personal commun., 1974). *L. ignotus* seems slightly more primitive than the latter in lacking posterior cingulids on the lower molars, in possessing higher protoconids on P_{2-3} , and a slightly more developed talonid on P_4 .

In contrast to *L. ignotus*, the lower canine in *L. notissimus* and *L. lacunatus* is large and recurved, P_2 and P_3 are more elongate and bear a small low

paraconid, the talonid on P_4 is relatively longer and wider, and the metaconid and protoconid on M_{1-3} are slightly more bulbous. The hypoconulid is not reduced on M_{1-3} of *L. notissimus* and *L. lacunatus*, the talonid basin is more nearly rounded than V-shaped, and the cristid obliqua is oriented less nearly parallel to the entocristid, compared to that of *L. ignotus*.

Russell, et al. (1975), alluded to the condylarthran nature of *Litolestes*, although they retained that genus in the Adapisoricidae. One of the problems of their review is the failure to discuss the genotype, *L. ignotus*. Only *L. notissimus* was considered. That species, as well as *L. lacunatus*, superficially resemble hyposodontids, mainly in the semibulbous nature of the molar protoconids and metaconids, compared to those of *L. ignotus*. However, in hyposodontids known to me the molars are considerably more robust and less angular in occlusal outline. M_2 is invariably larger than M_1 and M_3 , the molar paraconids are reduced to a simple ridge between the protoconid and metaconid, and P_4 is semimolariform or submolariform. As in *L. ignotus* and the Tepee Trail erinaceid, the lower molars of *L. notissimus* and *L. lacunatus* are not robust, they decrease progressively in size from M_1 to M_3 , the paraconid on M_1 is slightly compressed but is not reduced, and the paraconids on M_{2-3} are dorsally flattened but cusped.

L. notissimus and *L. lacunatus* are stratigraphically older than *L. ignotus*. As erinaceids, they have more plesiomorphic features than *L. ignotus*, e.g., the unreduced hypoconulid and a more nearly rounded talonid basin on the lower molars, and a slightly longer talonid on P_4 . Of interest is the large lower canine of *L. notissimus* and *L. lacunatus*, a feature absent in *L. ignotus* (Schwartz and Krishtalka, 1976) and later erinaceines (Butler, 1948), but retained in many echinosoricines (Butler, 1948). *L. notissimus* and *L. lacunatus* may represent the early echinosoricine condition in which a canine and four premolars are derived from a *Kennalestes*-like dental complement of a canine and five premolars. *L. ignotus*, on the other hand, with loss of the lower canine and retention of five premolars, may mirror the origin of the erinaceine lower dentition.

The known parts of the upper dentition of *L. ignotus* and *L. notissimus* (AMNH 33942, 33944) are less erinaceid-like than those of the lower dentition. P_4 in these species lacks a metacone, and is premolariform. M_{1-3} are typically adapisoricid-like: molars wider than long and shorter lingually than labially, narrow styler shelves, rectangular occlusal outline

with a shallow labial emargination and a constriction across the conules, conical or subconical paracone and metacone, well-developed conules with internal wings, a hypocone, and a weak anterior cingulum—characters that are plesiomorphic for many Paleocene eutherians like primates, lipotyphlan insectivores, pantolestids, apatemyids, and condylarths, and not indicative of phylogenetic relationships among taxa within these groups.

With regard to adapisoricids, two of the derived characters of upper molars of early erinaceids are the progressive reduction in size from M^1 to M^3 and the posterolabial position of the hypocone relative to that of the protocone—characters that occur in the Tepee Trail erinaceid. In *Litolestes*, the hypocone on M^{1-2} occurs more nearly posterior than posterolingual to the protocone. M^2 of *Litolestes* is not larger than M^1 to the degree seen in adapisoricids and hyopsodontids. Rather, M^2 is shorter than M^1 , and is slightly wider only in the area of the stylar shelf. In these respects the upper dentition of *Litolestes* approaches the typical erinaceid condition but is primitive relative to the upper dentition of the erinaceid from Tepee Trail.

Leipsanolestes Simpson, 1928

This genus is known only from the lower dentition of one species. Simpson (1928) originally described *L. seigfriedti* as an adapisoricid, but later (1929) referred *Leipsanolestes* to a subgenus of *Leptacodon*. McKenna (1960a) argued for inclusion of *L. seigfriedti* in *Entomolestes*, whereas Robinson (1968b) placed the species in *Talpavus*. Russell, et al. (1975), provisionally retained *Leipsanolestes* as a valid genus in the Adapisoricidae.

As described below, the molar morphology of *Leipsanolestes* is very similar to that of *Litolestes ignotus*, and differs from *M. nitens* and *Talpavus*, especially in those features that distinguish early erinaceids from adapisoricids.

Leipsanolestes seigfriedti Simpson, 1928

(Fig. 13; Table 7)

TYPE: AMNH 22157, RM₂₋₃, Fort Union Formation, Montana.

REFERRED SPECIMENS: CM 11517, LP₄-M₁; CM 11519, RP₄-M₁; CM 11532, LM₁; CM 11553, RP₄-M₃; CM 11662, LP₄, M₂; CM 11664, LP₄; CM 11676, RM₁; CM 11704, R1/2M₁-M₂; AMNH 56317, RM₁₋₃.

LOCALITIES: Bear Creek, Fort Union Formation, Montana; Reclusa Blowout, Powder River local fauna, Wyoming.

KNOWN DISTRIBUTION: Late Tiffanian, Montana; early Wasatchian, Wyoming.

DESCRIPTION AND REMARKS: Teeth anterior to P₄ are unknown. P₄ is semimolariform, with the talonid almost as long as the trigonid. The paraconid is bulbous, anterolingual, and as large as the metaconid. The metaconid occurs slightly higher than the paraconid on the posterolingual face of the protoconid. The talonid bears two tiny cusps, an entoconid and hypoconid, which, respectively, form the posterior tips of the long and parallel entocristid and cristid obliqua. The talonid basin between these two cristids occupies approximately one-half the width of the talonid.

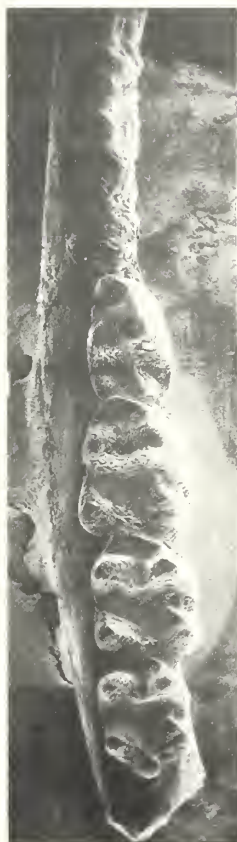
The molars of *Leipsanolestes seigfriedti* are low and rectangular, and decrease in size from M₁ to M₃, although not as radically as in *Litolestes ignotus*. The paraconid is fully cuspsate and is flattened dorsally to produce a low angular shelf. The protoconid and metaconid are blunt, conical cusps, and the talonid basin is developed as a V-shaped valley. The internal walls of the entoconid and hypoconid are flat, oriented ventromedially toward the talonid basin, and extend anteriorly to meet the trigonid. The hypoconulid is extremely reduced on M₁₋₂, but is discernible on the posterior edge of the entoconid, just lingual to the midline. As a result, the posterior margin of the talonid on M₁₋₂ is nearly straight, as is the case in *L. ignotus*, *Entomolestes grangeri*, and the late Eocene erinaceid from Tepee Trail.

Although *Leipsanolestes seigfriedti* and *Litolestes ignotus* were contemporaneous erinaceids, the former is more primitive in the retention of a semimolariform P₄ and the less-marked reduction in size of the molars from M₁ to M₃. However, the structure of the molars of *L. seigfriedti* is unquestionably erinaceid-like. This species may represent an early lineage of erinaceids that, with *Litolestes*, shared an early Paleocene or older ancestry from a form with a semimolariform P₄.

Delson (1971) erroneously referred AMNH 56317, partial right mandible with M₁₋₃ from the early Eocene Powder River local fauna, to *Entomolestes* cf. *nitens*. The molars are virtually identical to those of *L. seigfriedti* except for the complete loss of the hypoconulid on the Eocene form. This specimen is here



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A13
B

assigned to *L. seigfriedti*, although recovery of additional material may determine that AMNH 56317 warrants specific distinction from *L. seigfriedti*.

The confusion concerning the affinities of *Leipsanolestes* was not resolved in the recent discussion by Russell, et al. (1975). The authors compared this genus only to "*Entomolestes*" *nitens*, noted a number of diagnostic differences and concluded that the two species shared a special affinity among adapisoricids.

In comparison to *Macrocranium nitens*, P_4 of *Leipsanolestes* is semimolariform rather than premolariform. The talonid is more elongate and the talonid basin occupies one-half the width of the talonid. M_{1-3} of *Leipsanolestes* (and other erinaceids) are distinct from those of *M. nitens* (and other adapisoricids) in that they are more rectangular in occlusal outline and show a progressive reduction in size. The talonid on M_{1-2} of *Leipsanolestes* is not longer than the trigonid, the hypoconulid is extremely reduced, the talonid cusps occur posteriorly along the nearly straight posterior margin of the talonid, and the paraconid is a low, fully cusped, dorsally flattened shelf rather than a compressed lophid. *Scenopagus* and *Talpavus* differ from *Leipsanolestes* in the structure of P_4 , and in possessing higher, sharper, molar cusps, and a deeper hypoflexid notch.

As discussed below, among species previously classified by most authors as adapisoricids, *Entomolestes grangeri* bears the closest resemblance to *Leipsanolestes*.

?Erinaceidae

Entomolestes Matthew, 1909

Entomolestes grangeri Matthew, 1909

The taxonomic history of this genus was discussed in an earlier section. The genotype, *E. grangeri*, is known only from the holotype, AMNH 11485, partial left mandible with P_3 - M_3 , from the upper part of the Bridger Formation, Middle Eocene of Wyoming. Apart from Robinson (1968b), previous considerations of *Entomolestes* failed to distinguish between *E. grangeri* and "*E.*" *nitens*, which I have referred above to *Macrocranium*.

Unfortunately, the molars on AMNH 11485 are damaged, obscuring potentially diagnostic features. However, the lower dentition bears a number of discernible erinaceid characters. Five alveoli are preserved anterior to P_3 , and are interpreted by Robinson (1968b) to have been filled with I_{2-3} , C_1 , P_{1-2} , all single-rooted. Robinson also noted, however, that the alveolus for P_2 is elongate and slightly hourglass-

shaped, so that P_2 may have had two roots, as in other erinaceids. P_3 is double-rooted and has a low, blade-like, procumbent crown. P_4 is typically premolariform with an extremely short talonid and a single cusplule at the posterior tip of the cristid obliqua. The molars are low, rectangular in occlusal view, and lean anterolingually. M_3 is reduced, compared to M_{1-2} , which are of equal size. The talonids are as wide as the trigonids and not elongate, whereas the opposite is true in *M. nitens*. The paraconid, damaged on M_1 and M_3 , is low, somewhat compressed, and oriented anterolingually on M_2 . The metaconid and protoconid are quite worn, but appear to have been well developed and conical. The hypoflexid notch is shallow, as in other erinaceomorphs, since the cristid obliqua originates labially on the posterior wall of the trigonid. The entoconid is high, elongated anteroposteriorly, and has a flat internal wall that slopes ventromedially to the bottom of the talonid basin. A tiny notch occurs lingually at the junction of the high entocristid and the posterolingual face of the metaconid. The hypoconid is worn flat. The hypoconulid on M_{1-2} is reduced and occurs on the posterior edge of the entoconid, just lingual to the midline, as is also the case in *L. ignotus* and *Leipsanolestes*. As a result, the talonid cusps are lined up along the nearly straight posterior margin of the talonid.

These characters imply the erinaceid affinities of *E. grangeri*. Although M_1 and M_2 are equal in size, the molars of *E. grangeri* most closely resemble those of *Leipsanolestes*. Clearly, more complete *E. grangeri* material is needed before its relationships can be accurately assessed.

Erinaceidae: Summary

The two or possibly three known genera that comprise the North American early Tertiary record of erinaceids can be readily distinguished from adapisoricids and soricomorphs on the basis of dental remains. P_{2-4} are double-rooted, and P_4 is premolariform. The molars are rectangular in occlusal outline and decrease in size from M_1 to M_3 . The paraconid, more nearly erect and lingual on M_1 , is flattened dorsally into a shelf-like cusp on M_{2-3} and occurs closer to the midline. The protoconid and metaconid are low, conical cusps. The talonid basin is formed as a V-shaped valley by the flat internal walls of the hypoconid and entoconid. These cusps are also elongated anteriorly to the trigonid. The hypoconulid is extremely reduced on M_{1-2} and the hypoflexid notch is shallow.

In the earliest known erinaceid, *Litolestes*, some of these characters, like the structure of the talonid and the reduced hypoconulid, are less well expressed and imply the primitive condition. *Litolestes* and *Leipsanolestes* seem to represent two early, divergent lineages of

erinaceids. Species of the former seem suitable morphologically and temporally to be representatives of early erinaceine and echinosoricine erinaceids. *L. ignotus* may be close to the ancestry of the late Eocene erinaceid from Tepee Trail, Wyoming.

Table 7. Dimensions of lower teeth of *Litolestes ignotus* and *Leipsanolestes seigfriedti*

	P ₄			M ₁			M ₂			M ₃	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>L. ignotus</i>											
PU 13354	1.5	1.2	1.6	1.2	1.3	1.4	1.2	—			
PU 13974	1.7	1.2	1.7	1.3	1.3	1.5	1.3	1.3	1.3	1.0	0.9
PU 14064	1.6	1.2	1.7	1.2	1.2	1.5	1.2	1.2			
PU 14333	1.7	1.4	1.7	1.5	1.5						
PU 19362	1.7	1.4	1.8	1.5	1.5	1.5	1.3	1.3	1.4	1.2	1.0
PU 19387	1.8	1.3	1.8	1.4	1.4	1.6	1.4	1.3	1.4	1.0	0.9
Mean	1.67	1.28	1.72	1.35	1.36	1.48	1.28	1.28	1.37	1.07	0.93
<i>L. seigfriedti</i>											
CM 11517	1.5	1.0	1.8	1.4	1.5						
CM 11519	1.7	1.1	1.8	1.3	—						
CM 11532			1.6	1.4	1.4						
CM 11662	1.6	1.3				1.5	1.3	1.3			
CM 11676			1.8	1.3							
CM 11704			—	—	1.5	1.6	1.4	1.4			
AMNH 56317			1.7	1.2	1.3	1.6	1.3	1.4	1.4	—	1.1
Mean	1.60	1.13	1.74	1.32	1.42	1.57	1.33	1.37			

ACKNOWLEDGEMENTS

During the course of this study I have become deeply indebted to many individuals, most especially to Dr. Craig C. Black, for his warm friendship, constant encouragement, and critical counsel.

Dr. Black, Dr. Peter Robinson (University of Colorado), Dr. Malcolm C. McKenna (American Museum of Natural History), and Dr. Mary R. Dawson (Carnegie Museum of Natural History), originally suggested this study to me as a significant subject for a doctoral dissertation in vertebrate paleontology, and provided generous access to and loan of fossil material in their care.

I am also grateful to them and to the following for thoughtful and stimulating discussions concerning early Tertiary insectivore evolution: Dr. Percy M. Butler (Royal Holloway College, London), Dr. Jason A. Lillegraven (San Diego State University), Dr. Jeffrey H. Schwartz (University of Pittsburgh),

Michael J. Novacek (University of California, Berkeley), and Craig B. Wood (Harvard University). Dr. Lillegraven, Dr. McKenna, and Mr. Novacek kindly allowed the use of information from manuscripts in press. The pertinent insectivore material from the Polecat Bench collection was made available to me by Dr. Donald L. Baird (Princeton University), and Craig Wood.

I wish to thank Jack Capenos, Crucible Research Division, Colt Industries, Pittsburgh, for the scanning electron micrographs, and Elizabeth Hill for typing the manuscript.

This study was supported by teaching and research assistantships from the Department of Biology, the Graduate School and the Institute of Museum Research, Texas Tech University, and by a post-doctoral fellowship from Carnegie Museum of Natural History.

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Appendix A. Dimensions of lower teeth of *Scenopagus edenensis*, *S. curticens* and *S. priscus*

	P ₄			M ₁			M ₂			M ₃		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	
<i>S. edenensis</i>												
YPM 13612									2.5	1.8	1.4	
YPM 14932						2.6	1.9	1.9				
YPM 14934			2.3	—	1.9	2.5	2.0	1.8				
YPM 16910						2.7	2.2	2.0	2.7	—	—	
AMNH 11428			2.1	1.7	1.8	2.2	2.0	1.9				
CM 13739	2.0	1.6	—	1.9	—							
CM 13732						2.2	2.0	1.8	2.3	1.7	1.3	
CM 13734	2.0	1.4	—	—	—							
CM 13728						2.2	—	—	2.3	1.7	1.4	
CM 6444	2.1	1.5	2.3	1.9	—							
CM 6449			2.1	1.7	1.7	2.1	1.9	1.8	2.4	1.8	1.5	
CM 13731			2.3	1.7	1.7							
CM 13740						2.3	2.0	1.8				
CM 6441	2.0	1.5				2.3	2.0	1.9				
CM 17318	2.2	1.5	2.4	1.9	2.0							
CM 13737	2.0	1.5										
CM 13730	2.0	—	2.1	—	—	2.1	—	—				
CM 13729			—	—	1.9	2.2	1.9	1.8				
CM 13735	2.0	1.4										
CM 6485	2.2	1.4	—	1.8	—							
CM 13733						2.2	2.1	1.8				
CM 13736									2.4	1.7	1.4	
CM 13738	2.1	1.5										
CM 6443						2.1	1.9	1.8	2.3	1.7	1.3	
CM 17317						—	—	1.8	—	1.7	1.3	
TTU-P-5571						2.0	—	—				
TTU-P-5572									2.3	—	—	
TTU-P-7161			2.3	1.7	1.8							
TTU-P-7162			2.3	1.9	2.0							
TTU-P-7163			2.1	1.8	1.7							
TTU-P-7164			2.3	1.8	1.9							
TTU-P-7165			2.1	1.7	1.7							
TTU-P-7166			2.3	1.9	1.9							
TTU-P-7180						2.2	2.0	1.9				
TTU-P-7181						2.1	1.8	—				
TTU-P-7182						2.3	1.9	1.8				
TTU-P-7183						2.3	1.9	1.8				
TTU-P-7184						2.2	1.9	1.8				
TTU-P-7185						2.3	2.0	1.9				
TTU-P-7186						2.3	1.9	1.8				
TTU-P-7187						2.2	2.0	1.9				
TTU-P-7188									2.4	1.7	1.2	
TTU-P-7189									2.2	1.7	1.3	
<i>S. curticens</i>												
YPM 16913			1.8	1.6	1.6	1.8	1.6	1.4				
YPM 14939			1.9	1.5	1.5	1.8	1.6	1.5				
YPM 13610-1A	1.5	1.1										
YPM 13610-1B	1.5	1.2	1.8	1.5	1.6	1.8	1.6	1.5				
YPM 13610-2			1.7	1.4	1.5	1.7	1.5	1.4				
YPM 15255						1.8	—	1.4	1.6	1.2	0.9	
YPM 15254	1.5	1.2	1.8	1.5	1.6	1.8	1.6	1.5	1.6	1.2	1.1	
YPM 16912	1.5	1.2	1.7	1.6	1.5							
AMNH 12058						1.8	1.6	1.5	1.6	1.3	1.2	
AMNH 12055			—	—	1.5	1.8	1.7	1.5	—	1.3	—	

Appendix A. Dimensions of lower teeth of *Scenopagus edenensis*, *S. curticens* and *S. priscus*, continued

	P ₄			M ₁			M ₂			M ₃	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
<i>S. curticens</i>											
AMNH 12062			—	—	1.5	1.7	1.6	1.4	—	1.2	—
AMNH 12064	1.5	1.2	1.8	1.5	1.5						
AMNH 11491			2.0	1.5	1.5						
AMNH 48183	1.6	1.2				1.9	1.5	1.6			
AMNH 59643			2.0	1.5	1.6						
UCMP 96155			1.7	1.4	1.5	1.7	1.5	1.4	1.7	1.3	1.0
TTU-P-3928			—	—	1.6	1.7	1.6	1.5	1.5	1.3	1.0
TTU-P-7054			1.8	1.4	1.5						
<i>S. priscus</i>											
AMNH 56060			1.4	1.1	1.2	1.5	1.3	1.2	1.3	0.9	—
AMNH 55156	1.3	1.0	1.5	1.3	1.3						
CM 13753	1.3	1.0	1.5	1.2	1.2						
CM 13749			1.5	1.2	1.2	1.4	1.3	1.1			
CM 13750	1.3	0.9	1.5	1.2	1.3						
CM 13744	—	1.1									
CM 17316						1.4	1.3	1.1	—	1.1	—
CM 13746			1.5	1.1	1.1						
CM 13743						1.5	—	—	1.3	0.9	0.8
CM 13748			1.5	1.1	1.1	1.5	1.5	1.1	1.0		
CM 6486	1.2	0.9	1.5	1.1	1.2	1.4	1.2	1.0			
CM 17319						1.5	1.2	1.0	1.3	1.0	0.7
CM 13751	1.3	0.9	1.4	1.3	1.3	1.4	1.3	1.1			
CM 13752	1.4	0.9	1.5	1.1	1.3						
TTU-P-7094			1.4	1.0	1.2						
TTU-P-7098			1.3	0.9	1.0						
TTU-P-7099			1.4	1.1	1.2						
TTU-P-7097			1.4	1.0	1.1						
TTU-P-7096			1.3	0.8	0.9						
TTU-P-7100			1.3	0.9	1.0						
TTU-P-7082			1.4	0.9	1.0						
TTU-P-7092			1.5	1.0	1.1						
TTU-P-7093			1.3	0.9	—						
TTU-P-7081			1.4	0.9	—						
TTU-P-7083			1.4	0.9	1.0						
TTU-P-7084			1.5	1.1	1.1						
TTU-P-7085			1.5	1.0	1.1						
TTU-P-7090			1.4	1.0	1.0						
TTU-P-7095			1.4	1.0	1.0						
TTU-P-7087			1.5	1.0	1.1						
TTU-P-7086			1.5	1.0	1.1						
TTU-P-7088			1.4	1.0	1.1						
TTU-P-7120			1.4	0.9	1.0						
TTU-P-7121			1.4	1.0	1.0						
TTU-P-7119			1.5	1.1	1.0						
TTU-P-7124						1.5	1.2	1.0			
TTU-P-7125						1.4	1.1	0.8			
TTU-P-7117						1.6	1.2	0.9			
TTU-P-7118						1.5	1.2	1.0			
TTU-P-7089						1.4	1.2	1.1			
TTU-P-7122						1.4	1.2	1.1			
TTU-P-7129						—	—	—			
TTU-P-7131						1.4	1.1	1.0			
TTU-P-7132						1.5	1.3	1.1			

Appendix A. Dimensions of lower teeth of *Scenopagus edenensis*, *S. curticens* and *S. priscus*, continued

	P ₄			M ₁			M ₂			M ₃		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	
<i>S. priscus</i>												
TTU-P-7130						1.4	1.1	1.0				
TTU-P-7126						1.4	1.2	1.1				
TTU-P-7127						—	1.1	—				
TTU-P-7128									1.3	0.9	0.7	
TTU-P-7123									1.4	0.9	0.7	
TTU-P-7140									1.5	1.0	0.8	
TTU-P-7137									1.4	0.9	0.7	
TTU-P-7138									1.3	1.0	—	
TTU-P-7139									1.3	0.8	0.6	
TTU-P-7135									1.3	0.9	0.7	
TTU-P-7142									1.4	1.0	0.7	
TTU-P-7134									1.3	—	—	
TTU-P-7141									1.3	1.0	0.7	
TTU-P-7143									1.3	1.1	0.8	
TTU-P-7136									1.3	0.9	0.7	

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BULLETIN

of CARNEGIE MUSEUM OF NATURAL HISTORY



THE CLARK'S CAVE BONE DEPOSIT AND THE LATE PLEISTOCENE PALEOECOLOGY OF THE CENTRAL APPALACHIAN MOUNTAINS OF VIRGINIA

JOHN E. GUILDAY, PAUL W. PARMALEE, HAROLD W. HAMILTON

NUMBER 2

PITTSBURGH, 1977

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DEDICATED TO THE MEMORY OF DR. J. KENNETH DOUTT,
CURATOR OF MAMMALS, CARNEGIE MUSEUM OF NATURAL HISTORY,
FROM 1938 TO 1972

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BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 2, pages 1-88, figures 1-21, tables 1-23

Issued January 19, 1977

Price: \$12.00 a copy

Publications Committee

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CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213

CONTENTS

Abstract	5
The Site	5
The Deposit	5
Procedure	6
Abbreviations and Acknowledgments	9
Regional Setting	10
History of Site	11
Clark's Cave Raptors	15
Quantitative Analysis	16
Faunal List	19
Biotic Discussions	
Flora	24
Decapoda—Crayfish	24
Insecta—Insects	24
Mollusca—Snails and Clams	24
Pisces—Fish	25
Amphibia—Amphibians	25
Reptilia—Reptiles	27
Aves—Birds	27
Mammalia—Mammals	39
Faunal Comparisons—Methods of Deposition	71
Ecological Interpretation	73
Bird Summary	73
Mammal Summary	74
Age of Deposit	77
The Late Glacial Environment	78
Life Zone Integrity	80
Literature Cited	83



Fig. 1. Looking north from Entrance No. 2, Clark's Cave, Bath County, Virginia, across Cowpasture River. Tower Hill Mountain in background. Fossil deposit in passageway left off photo. Sketch by J. R. Senior from H. Hamilton composite photo.

ABSTRACT

Remains of 142 species of vertebrates, ca 4,984 individuals, and 35 species of invertebrates, ca 5,547 individuals, were recovered from a late Pleistocene "owl roost" in the entrance talus of Clark's Cave in the central Appalachian Mountains, lat. 38°05'10" N., Bath County, Virginia, U.S.A. Sixty-four percent of the medium-to-small-sized mammals represented in the cave remains are now found either farther north or conform in size to present boreal population equivalents (Bergmann's Response) and with the New Paris No. 4, Pa. local fauna. Deposition took place during late glacial times, > 10,000 years B. P., and ceased before the boreal-to-temperate, post-glacial floral adjustment was completed at the site. Ptarmigan, *Lagopus*, and least chipmunk, *Eutamias*, are added to the

late glacial fauna of the Appalachians.

A spruce/pine parkland with nearby bog and meadowlands in a complicated topographical pattern is suggested by the ecological requirements of the faunal components. A contemporaneous mixture of presently allopatric northern, midwestern, and temperate Appalachian species is noted, suggesting a richer ecological picture than was apparent at New Paris No. 4, Pa., 240 km to the north.

Quantitative analysis suggests that several species of raptors were involved. Comparisons with other Appalachian cave and fissure deposits demonstrate the difficulty of ascertaining methods of deposition by faunal analysis only.

INTRODUCTION

THE SITE

Clark's Cave, 12 km southwest of Williamsville, Bath County, Virginia (U.S.G.S. Williamsville quadrangle 15' series, latitude 38°05'10" N., longitude 79°39'25" W.), is located in north-central Virginia on the south bank of the Cowpasture River in the headwaters of the James River drainage (Fig. 2). It is a large cave with a complicated maze of over 2,400 m of cave passages. The six major entrances to the cave occur along a one km strip of high, picturesque, limestone cliff that towers some 30 m above the southern bank of the river. The lower Devonian limestone cliffs, (Helderberg group, New Scotland member (Bick, 1962) form a distinctive feature of the landscape (Figs. 1 and 6). Extensive talus at their base, still active because of steep profile and crumbling cliff, forms a high, rocky tumble, forested, cool and shaded by the northward-facing cliffs. The cliff face and its numerous cave entrances make ideal roosts for birds of prey. Although no raptors nest in the cave entrances today, the barn owl (*Tyto alba*), red-tailed hawk (*Buteo jamaicensis*), and raven (*Corvus corax*) still frequent them as a temporary roost. These cliffs attracted raptors during the late Pleistocene. The extensive bone deposit here reported from entrance No. 2 (Fig. 3) represents but a small portion of a formerly more extensive accumulation of nesting and roosting debris.

Facing north across the Cowpasture River from the large amphitheater of entrance No. 2 (Fig. 1), about 20 m above the river, one looks across approximately 50 m to a gradually rising pasture at about the same

elevation (ca. 448 m, or 1,495 ft). One and one-half km beyond, the southern end of Tower Hill Mountain ascends to approximately 840 m (2,800 ft) elevation. Warm Springs Mountain, 6.4 km west of the cave, rises to an elevation of over 1,100 m. About a kilometer up- and down-stream from the cliffs (Figs. 8 and 9) the Cowpasture River broadens considerably, meandering across a flat valley floor, averaging .6 km wide, abruptly bordered by forested hills. These river flats were undoubtedly the source of most of the vertebrate fossils in this vole-dominated assembly. The rock inhabitants probably came from the talus immediately below the cave.

THE DEPOSIT

The fossil deposit, the Clark's Cave local fauna (Field Site No. 3, Figs. 4 and 5), was discovered near the top of a loose, unconsolidated talus feeding down from a passageway that entered the amphitheater of entrance No. 2 from the west (Figs. 4 and 5). Beginning in darkness, this talus cascaded at a 45° angle some 10 m, where it joined the main amphitheater talus fronting the cliffs. When first examined in the spring of 1972, bone fragments were noted throughout the talus accumulation. But the rare coincidence of unusually heavy rains that summer, coupled with a heavy rockfall from the cliff face above, caused a rock slide that removed three-quarters of the fossiliferous matrix. Only that portion that lay at the top of the talus was left intact.

An excavation (Figs. 4, 5 and 7) 2.1 m x 1.4 m x 0.5 m, approximately 3.9 cubic m, was made at the top of the talus in the fossiliferous area. The matrix

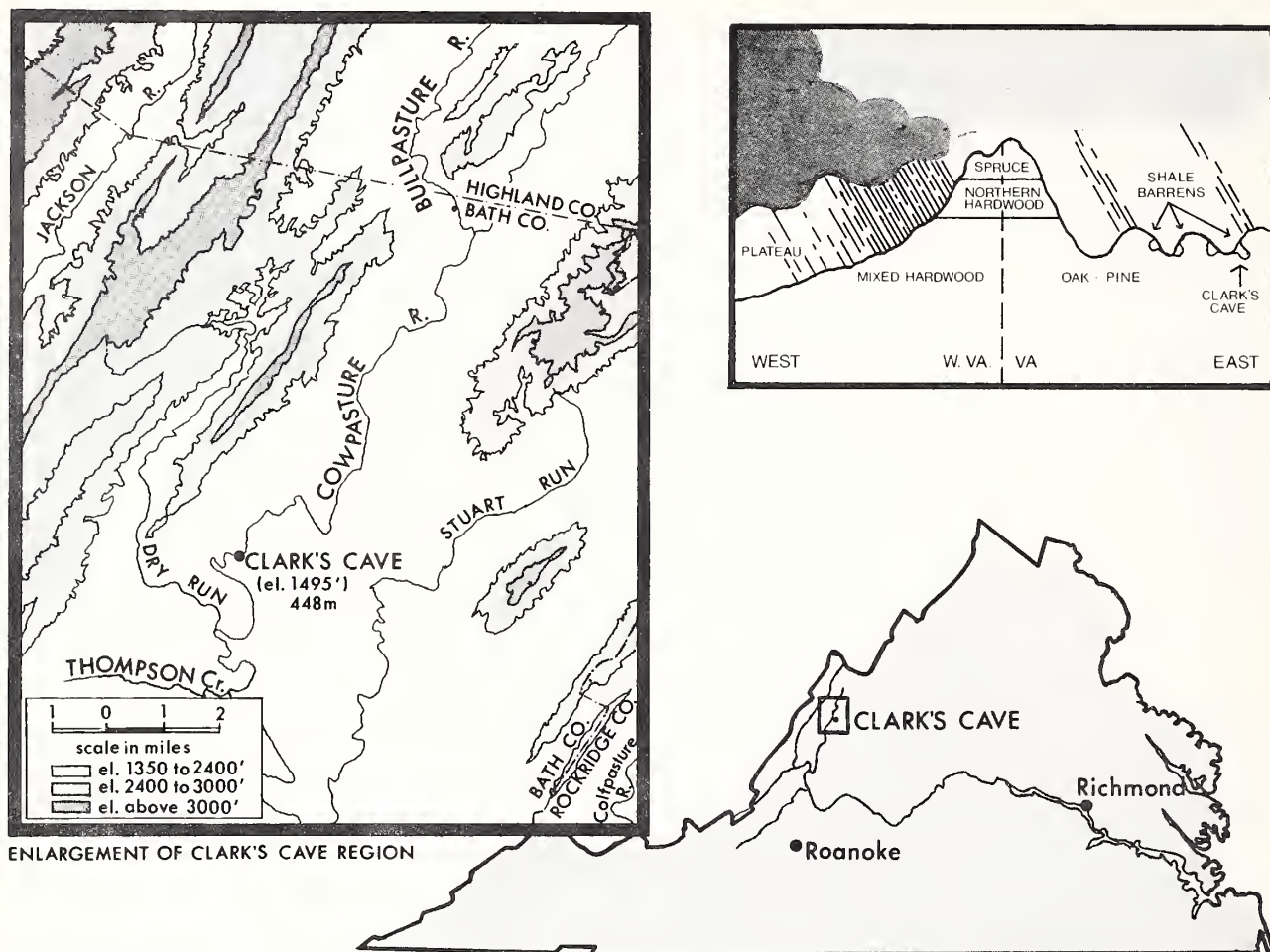


Fig. 2. Site location, Clark's Cave, Bath County, Virginia. Upper right: exaggerated cross-section of mid-Appalachians showing precipitation pattern, modified from Core, 1974.

was 90% cliff-wastage—ungraded, loose, frost-wedged fragments of Helderberg limestone, ranging in size from tiny spalls to large blocks. The remaining 10% consisted of organic remains and a dark-brown, dry soil-like material, probably worked into the raw talus by wind and gravity accretion. Open cracks between the rocks permitted material to filter down through the limits of the talus prior to and during excavation. The detritus varied from 30 cm to 46 cm in depth and rested on sterile cave clay. Organic inclusions (occurring throughout) were seeds, leaves (see floral listing), woodrat droppings, snails, egg-shell fragments, arthropod chitin, and thousands of small bones and teeth. No Recent owl pellets were encountered during excavation. There was no evidence of hair or feathers that occur in Recent owl pellet accumulations. These had apparently decomposed through the years, leaving only a lag deposit of bones and teeth of prey items.

PROCEDURE

Approximately 540 kg of matrix was dry-screened through a 6 mm mesh (1/4-inch hardware cloth) and large items were removed and boxed at the site. One hundred-eighty kg of screen-concentrate was bagged and washed through 1 mm mesh (commercial window-screening) at the New Paris field laboratory. All macroscopic organic inclusions were removed. Further sorting of bones and teeth was carried out at Carnegie Museum under the direction of Helen McGinnis and the senior author, and various categories were submitted to specialists for identification (see *Faunal List*). All specimens, with the exception of a few passenger pigeon remains, are stored in the Section of Vertebrate Fossils, Carnegie Museum of Natural History. Selected pigeon bones are stored in the avian osteology collection, Department of Anthropology, The University of Tennessee at Knoxville.

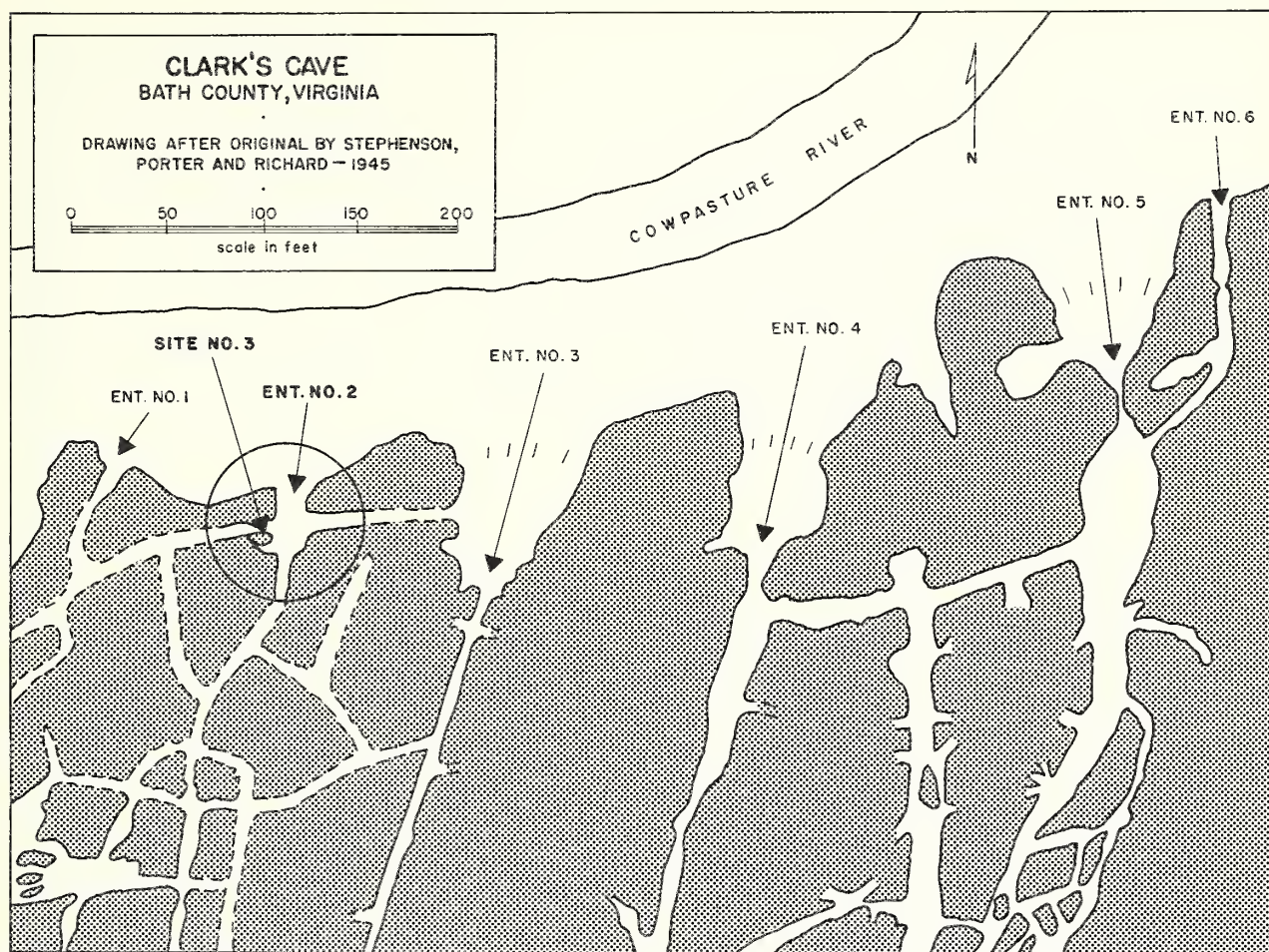


Fig. 3. Map of entrances to Clark's Cave, Bath County, Virginia.

ville. The loose nature of the matrix and its exposed situation made pollen analysis and carbon-14 dating (see *Age of Deposit*) unreliable. A carbon date was run on small mammal bones, and the woodrat droppings were saved for possible pollen content.

The three primary study objectives were: 1. Identification to species if possible; 2. Establishment of minimum numbers of individuals for each taxon; 3. Assessment of possible size-differences between fossil and Recent population equivalents. In the case of mammals these objectives were accomplished by studying the dentitions and cranial parts. Mammalian post-cranial material, with a few exceptions like talpid humeri, received only cursory attention. They were not classified or catalogued, but they are stored with the collection. Bird, reptile, amphibian, and fish identifications were based primarily on postcranial elements.

The minimum number of individuals of each spe-

cies (MNI) was established by the highest replication of any diagnostic elements—tooth, limb bone, etc. These elements differed from species to species. The voles, for example, were represented primarily by isolated teeth and partial maxillae and dentaries. Approximately 17,000 isolated arvicolid molars were recovered from the screen washings. Individual molars were specifically identified, then tallied according to their serial position, first, second, third molars, whether upper or lower, right or left. These categories were then tallied and the greatest number for any given tooth was considered the minimum number of individuals represented for that particular species. The same procedure utilizing various skeletal parts was employed for the entire vertebrate collection. Elements utilized are listed under materials in the individual species accounts.

Preservation of bones and teeth was chemically excellent, but mechanically poor. Bone appeared

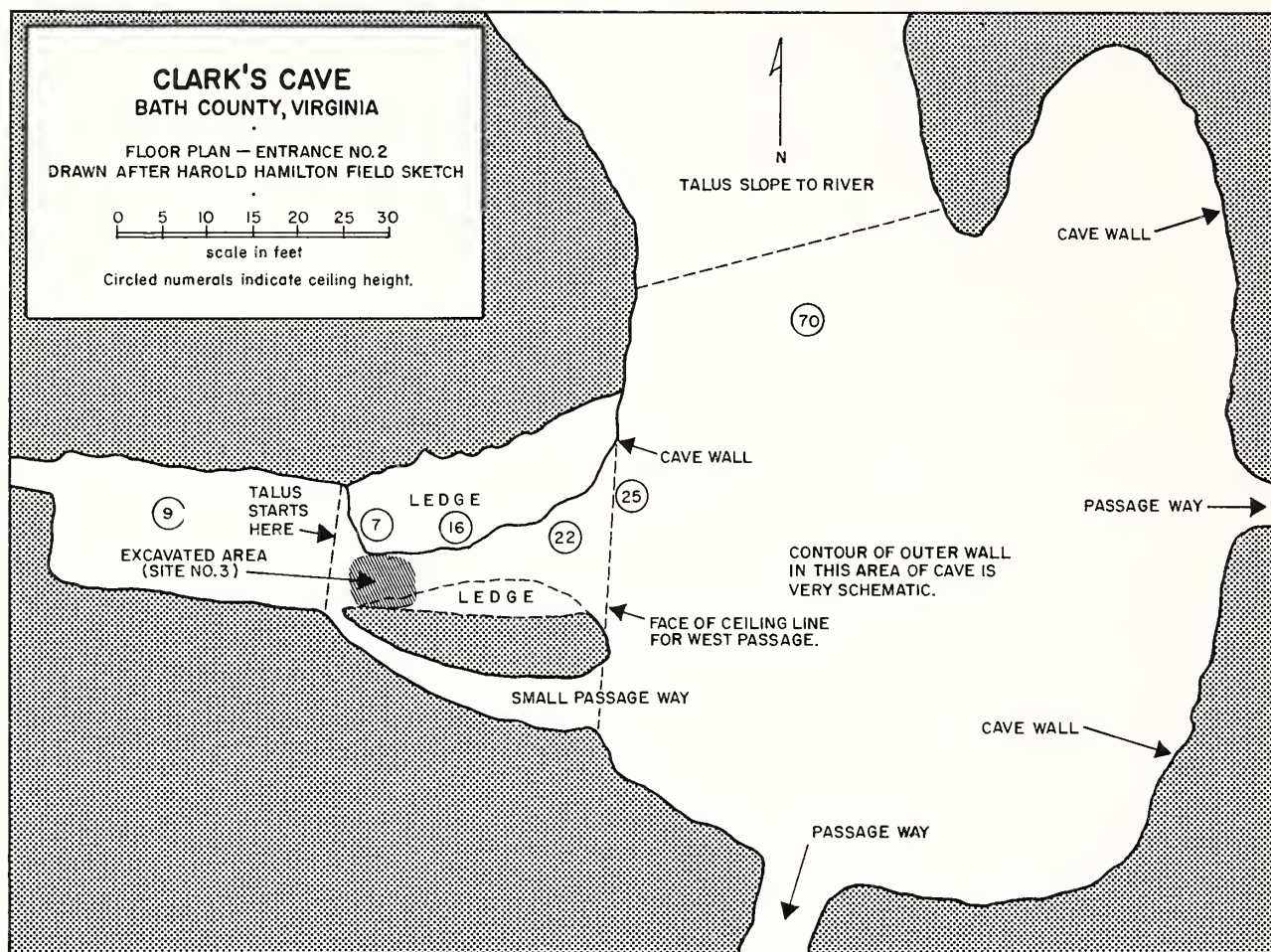


Fig. 4. Excavation plan, Entrance No. 2, Clark's Cave, Bath County, Virginia from above.

unaltered and frequently could not be distinguished from Recent owl pellet material from the area. Some specimens did have a thin carbonate crust, but none were fused. Bones, shells, and egg shells were badly broken, often ground to fragments on the sharp rock matrix by talus creep and excavating and recovery procedures. Very small specimens—shrew and bat dentaries, small molluscs—fared best, but larger objects were invariably badly fractured. Teeth, large or small, were usually separated from skull parts. No articulated remains were found. Size sorting was not present and all bone distribution, both horizontal and vertical, in the deposit appeared to be random.

Measurements less than one centimeter were taken with the aid of a Spencer Cycloptic stereoscopic microscope, using an ocular grid at 10 X. The particular instrument used (No. 4451931) required a correction factor of 0.97 to convert ocular measurements to true millimeters at that magnification.

Larger measurements were taken with a dial micrometer calibrated to 0.1 mm.

Responsibility for various sections are as follows: geology and site mapping, Hamilton; birds, Parmalee; mammals, Guilday. Remaining sections are by Parmalee and Guilday jointly. Specialists involved in identifications are listed in *Acknowledgements* and in the faunal list.

To avoid repetition, previously reported bone sites are not cited in the text. References may be found in Table 23 (site references).

Avian nomenclature follows the A.O.U. *Checklist of North American Birds* (5th edition) and its 32nd supplement (Auk 90:411-419). Mammalian nomenclature is largely from Jones, Carter, and Genoways, 1975.

The bird bones from Back Creek Cave No. 2, Bath Co., Virginia, are included in the inventory of bird remains, but are catalogued and listed separately

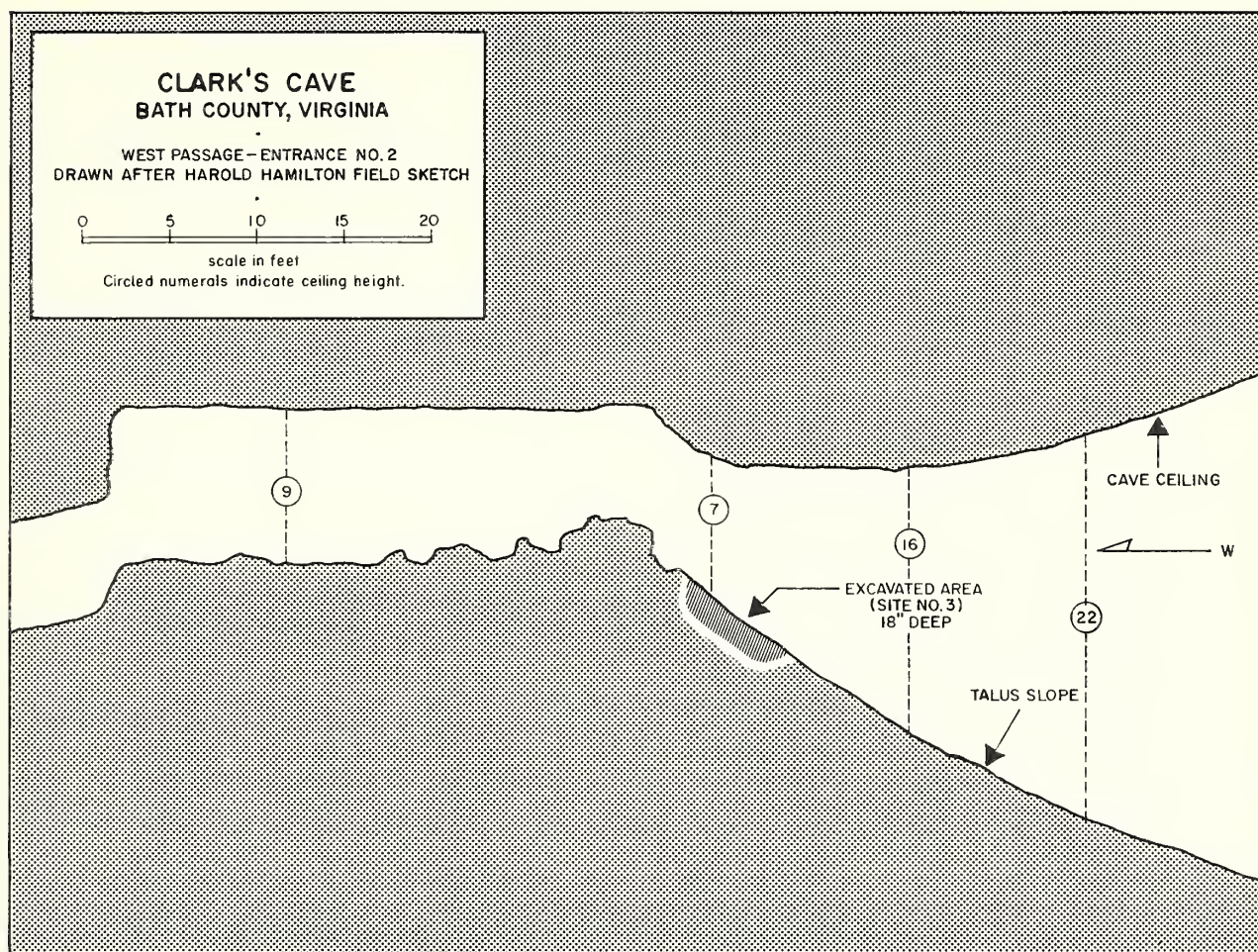


Fig. 5. Excavation plan, Entrance No. 2, Clark's Cave, Bath County, Virginia vertical section.

under appropriate species. This site, a shallow "rock shelter" 24 km west of Clark's Cave, is a late Pleistocene owl roost deposit similar to that at Clark's Cave. Most of the mammals have not yet been studied as of this time, but the faunal make-up of the two sites appears to be similar.

ABBREVIATIONS

AMNH—American Museum of Natural History; B.P.—before present; ca—approximately; CM & CMNH—Carnegie Museum of Natural History; cm—centimeters; CV—coefficient of variation; g—grams; I—Isotopes, Inc.; kg—kilograms; km—kilometers; m—meters; MNI—minimum number of individuals; N—sample size; OR—observed range; SD—standard deviation; SI—Smithsonian Institution; USNM—United States National Museum; SIU—Southern Illinois University; \bar{X} —arithmetic mean; > —greater than. Capital and lower-case letters followed by on-

line numbers [C/c (canine), P/p (premolar), M/m (molar)] refer to upper and lower teeth, e.g., M1,m1.

ACKNOWLEDGMENTS

We are indebted to many people who contributed services and expertise to this project, and take great pleasure in acknowledging their assistance. Mrs. W. G. Clark, the owner of Clark's Cave, kindly allowed us to excavate and collect on her property. Able assistance during excavation and field screening was provided by Lee Ambrose, Alan Bailey, Mr. and Mrs. Nevin C. Davis, Karen Downing, Gwen Foster, Mary Ann Gross, Rita and Allen Hamilton, Paul, Helen, and Mimi Imblum, Mr. and Mrs. William King, and Mr. and Mrs. Robert New. Processing of matrix at the New Paris field laboratory under the co-direction of Allen D. McCrady and Harold W. Hamilton involved so many willing volunteers that space permits only a general, but warm thank-you to all. Helen

McGinnis deserves our special thanks for her many months of laboratory sorting and for the study and identification of the anuran remains.

We thank our many colleagues for their assistance: *Plants*: Fel Brunett, Chippewa Nature Center, Midland, Mich. *Molluscs*: Leslie Hubricht, Meridian, Miss.; Dr. William J. Clench, Harvard University. *Decapods*: Dr. Horton H. Hobbs, Jr., USNM. *Insects*: Dr. Everett D. Cashatt, Illinois State Museum. *Fish*: T. N. Todd and Dr. Robert R. Miller, University of Michigan. *Reptiles and amphibians*: Dr. Clarence J. McCoy, Jr., CMNH. *Birds*: Dr. Mary H. Clench and Dr. Kenneth C. Parkes, CMNH; Dr. Storrs L. Olson, Dr. Richard L. Zusi, and Dr. Alexander Wetmore, USNM; Dr. Amadeo M. Rea, University of Arizona, Tucson. *Mammals*: Dr. Elaine Anderson, Denver; Caroline A. Heppenstall, Dr. J. K. Doult, and Dr. Duane A. Schlitter, CMNH; Dr. Karl Koopman, AMNH; Dr. E. C. Galbreath, SIU; Wayne E. Clark, Assistant Archaeologist, Virginia State Library (who supplied archaeological data). Illustrations are by Erica Hanson (Fig. 19), James R. Senior (Figs. 1 - 5, 16) and Nancy Perkins (Figs. 11 - 15, 17, 18, 20, 21). Elizabeth Hill, Wendy Pollock, Kathleen Guilday, Albert Kollar, and Ronald Wilson provided laboratory or clerical assistance. We wish to thank Dr. Mary R. Dawson, CMNH, Dr. Charles O. Handley, Jr., USNM, and Dr. Holmes A. Semken, University of Iowa, for reviewing the manuscript. Dr. Handley also surveyed the Recent small mammals from the area, and we thank him for his many notes on the Recent vegetation, birds and mammals of the cave area, and for the loan of specimens. The authors are indebted to their wives, Alice, Barbara, and Rita, for things innumerable. Research was conducted under NSF Grant No. GB 42258, awarded to the senior author.

REGIONAL SETTING

The Cowpasture River rises in the central Appalachian Mountains. It meanders southwestward for some 72 km in an intermontane valley to join the James River, which flows east 400 km to the Atlantic Ocean. For most of its length, the valley of the Cowpasture River is broad and flat, averaging perhaps 0.8 km in width. In Bath County, Tower Hill Mountain, rising to 970 m, borders the northwestern side of the valley. The mountain crest follows an anticlinal ridge of the resistant Middle Silurian Clinton Formation, a heterogeneous mixture of sandstones and shales. The southeastern rim of the valley is formed by Shenandoah Mountain, a resistant synclinal core of Up-

per Devonian Chemung sands and conglomerates. The river follows the more easily eroded trough between these mountains. Sixteen km northeast of the cave Shenandoah Mountain rises to over 1,060 m but loses altitude to the south. Approximately two km directly south of the cave, a dissected range of hills, "the spurs," rises to 760 m.

About 1.5 km upstream from Clark's Cave, the river, flowing along the flat valley floor (Figs. 9 and 10), has worn through the structurally older Ridgeley sandstone and flows through an abruptly tightened valley, narrow and precipitous, carved out of the underlying Lower Devonian Helderberg limestone. The Cowpasture valley retains this gorgelike character past the cave mouth and for another km downstream, where the valley suddenly broadens again (Fig. 8) as the river emerges once more into shale lands.

High mountainous country west of the Cowpasture River valley, rising to over 1,000 m, diverts much of the moisture from the prevailing westerlies, and the valley lies within their rain shadow. This produces a mild xeric effect that has resulted in the formation of a distinct topographically and botanically defined provincial subdivision: the shale barrens. Shale barrens occur along the crests of low shale hills that lie just to the east of the plateau country, from southern Pennsylvania to southern Virginia (Keener, 1970).

The present climate of the area is temperate and mild. Observations over a forty-year period at Hot Springs, Bath County, 20 km southwest of the cave, show a temperature range from 36.7° to -28.9° C. (98° to -20° F.) with a January average of 0.2° C. (32.4° F.), and a July average of 20.8° C. (69.5° F.). There is no definite wet or dry season, but precipitation at Hot Springs is highest in June and lowest in January, with a yearly average of 105 cm. The weather is controlled by a succession of cyclonic pressure cells from the west, with (especially in the summer months) warm, moist air masses from the Caribbean, resulting in a varied day-to-day climatic pattern. Western Virginia is too far inland for its climate to be directly affected by the Atlantic Ocean except during rare hurricane phenomena. Winters are generally mild, except in the mountain and plateau highlands. Yearly snowfall averages 63.5 cm and usually does not provide continuous winter cover (Hibbard, 1941).

Just prior to Colonial settlement, the area surrounding the cave was completely forested with an oak-dominant vegetation (Braun, 1950; Hack & Good-

lett, 1960; Clarkson, 1966; Core, 1974). The slope on which the cave is located was undoubtedly covered, then as now, with a mesic Appalachian cove forest: hemlock (*Tsuga*), arborvitae (*Thuja*), tulip poplar (*Liriodendron*), and basswood (*Tilia*). This same forest is found in gorges on Tower Hill Mountain and Warm Springs Mountain, west of the cave. The nature and composition of the forest is in subtle concordance with local variations in elevation, exposure, drainage patterns, and soils. As a general rule, valley floors and higher mountain summits receive the most moisture, the former from precipitation plus slope drainage, the latter through precipitation alone. Valley floors of the area originally were covered with a white-oak (*Quercus alba*)-dominant forest, while the dryer mountain slopes were covered with a chestnut/chestnut-oak (*Castanea/Quercus prinus*)-dominant forest. In higher, moister, mountainous areas, and especially in high valley heads, the forest became richer in species of maple (*Acer*) and birch (*Betula*).

Spruce (*Picea*)-dominated woodland occurs, or did occur, on many of the higher summits to the west, but not near the Cowpasture River valley. The distinctive shale barrens, open woodlands of low scrub oak (*Quercus ilicifolia*) and pines (*Pinus*, spp.) with much bare ground, occupy the low hills bordering the southeastern rim of the valley (Fig. 9), forming a distinct biotype characterized by many low-order plant endemics. The shale barrens appear today as a distinct, open, mildly xeric habitat. They would certainly have been in the cruising range of the Clark's Cave raptors if they were in existence during the late Pleistocene. The presence of plant endemics argues that the barrens are at least that old, and they may have supported some of the Midwestern forms present in the deposit, like the sharp-tailed grouse (*Pedioectes phasianellus*), the least chipmunk (*Eutamias minimus*), and the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*).

The floor of the Cowpasture River valley, like that of the broad Shenandoah valley to the east, lies within the Carolinian Life Zone (Dice, 1943). This zone occupies the valley floors of western Virginia up to about 460 m and ascends to 600 m in open country. Its upper limit may dip as low as 370 m, however, in forested ravines (Murray, 1945). All the mountain ridges, with the exception of a few summits above 1,200 m, lie in the Alleghenian or Transition Zone. According to Murray, the theoretical upper limits of the Alleghenian Life Zone should lie between 915 m and 1,070 m in Virginia. But biological

zonation is not a simple function of altitude. It varies with slope exposure, air drainage, local precipitation, and soil characteristics. Zones merge gradually, and the upper limits of the Transition Zone in the Virginia and West Virginia mountains range from 1,000 m (Cranberry Glades, W. Va.) to 1,364 m (Elliott's Knob, Va.). Areas of Canadian Zone, spruce-dominated flora top a few of the higher peaks.

"While there is a good deal of Canadian Zone territory in the high Allegheny Plateau of West Virginia [700,000 acres before logging, Brooks, 1943, p. 25], and a fair area of it on the great peaks of the Smokies along the North Carolina and Tennessee line there is little or no territory in Virginia which can be called pure Canadian. On White Top and Mt. Rogers, the two highest mountains in Virginia which reach 5,519 [1,672 m] and 5,720 feet [1,723 m] respectively, we have some small areas which are practically Canadian, and on Middle Mountain in Highland County we have some territory that approaches it." (Murray, 1945 : 20) After logging, the Canadian Zone spruce stands are replaced by Transition Zone mixed hardwood/coniferous forest.

It can be seen that great topographic and biotic diversity, ranging from mountain tops to valley floors, and great variations in subsurface water, ranging from the xeric shale hills of the shale barrens to river flood plains, were present within the cruising range of the Clark's Cave raptors. Thus the interpretation of the fossil fauna from a regional point of view is complicated.

HISTORY OF SITE

The history of man's occupation of the Cowpasture River valley may be related to the age of the fossil deposit. Unmolested, the nesting of birds of prey at the site could proceed with little interruption. But the arrival of man in the valley may have brought nesting to an end because the former raptor roost at entrance No. 2 was easily accessible from the river. The fauna recovered from the site suggests that deposition ceased prior to the establishment of the modern regional biota about 10,000 to 11,000 years ago, and current archaeological evidence suggests that paleo-Indian occupation of western Virginia extended at least that far back in time. No direct evidence of such an early occupation has been recorded from the Cowpasture valley, but an important paleo-Indian complex, the Thunderbird Site (44 WR 11) (Gardner, 1974), is known from the Shenandoah valley, about 70 km to the east. This site, on an alluvial fan of the South Fork Shenandoah



Fig. 6. View looking southeast, from across Cowpasture River, at Clark's Cliffs, early Devonian Helderberg limestone. Entrance No. 2 and fossil site off photo to right. Note active, wooded talus. Hamilton photo.



Fig. 7. Mary Ann Gross (lower left) on excavation site in unconsolidated talus of west passage, Entrance No. 2, Clark's Cave, Bath County, Virginia.



Fig. 8. Cowpasture River, 2 kilometers downstream from Clark's Cave, Bath County, Virginia. Cave is behind hill to right. Note V-shaped gorge as river traverses Helderberg limestone, and flat valley floor as it emerges into shale lands.

River, is centered around an aboriginal jasper quarry from which paleo-Indian hunters periodically refurbished their tool kits. The easy access to Clark's Cave roosts may have invited exploitation and disruption at an early date, forcing the birds to seek more secure nesting sites.

Four prehistoric archaeological sites in the Cowpasture River valley itself are recorded in the Virginia State Library archaeological survey site records (site nos. 44 HL 12, 44 HL 14, 44 BA 1, 44 BA 36). One, 44 BA 1, is in a setting quite similar to the Clark's Cave cliffs. It is a rockshelter in a small gorge formed where the Cowpasture River traverses a tongue of Devonian limestone that crosses the river valley 13 km down stream from Clark's Cave. Other small Indian campsites are recorded from the nearby Bullpasture and Jackson River valleys (MacCord, 1973a, 1973b).

The valley was surveyed in the early 1740's fol-

lowing a short period of Indian wars, and permanent European settlement began. Timber was cleared first in the valley floor and then in the surrounding mountains. The valley soon became a farming and livestock area. The cave became the site of a thriving saltpeter industry established to satisfy the demand for the substance in gunpowder manufacture. Clark's Cave is reputed to have had over 200 men mining cave earth (Faust, 1964). With the decline of the saltpeter industry at the close of the Civil War in 1865, the site was left relatively undisturbed. It was surrounded by farming activities and was occasionally visited by the public. It later became a popular resort of weekend cave explorers, but was closed to caving in 1973.

In summary, Clark's Cave and the Clark's cliffs have been exposed to potential human exploitation for at least the past 10,000 years. Any evidence of an actual Indian occupation at any of the entrances of

Clark's Cave would have been destroyed by mining activities, and we are indeed fortunate that site No. 3 was not destroyed as well. Only its location, perched high on a talus slope in a dead-end passage, preserved it.

CLARK'S CAVE RAPTORS

The fossil bone deposit accumulated in the twilight zone of the cave around the roosts and nests of carnivorous cliff/cave-frequenting birds, primarily owls. The bulk of the deposit represents prey collected from the neighboring environs and is the result of the build-up of food debris, primarily owl pellets, through the course of many years. The variety of prey, nocturnal and diurnal, field and forest, vertebrate and invertebrate, argues for not one, but probably many species of birds of prey. Owls, hawks, eagles, vultures, ravens—all cliff-frequenting species—may have contributed at one time or another to the deposit. Raptor bones actually recovered included those of two accipiters, one falcon, and three owls—the great-horned, *Bubo virginianus*; the long-eared owl, or short-eared owl, *Asio*, sp.; and saw-whet owl, *Aegolius acadicus*, the latter possibly a prey item.

Large owls like the snowy owl, *Nyctes scandiaca*, and the great-horned owl prefer larger game than do smaller species like the short-eared owl; the barred owl, *Strix varia*; or the barn owl, *Tyto alba*. When the prey items of the Clark's Cave deposit are classified according to the size of the living animals, the collection resembles that of the prey of medium-sized field-hunting owls, the barn owl, and the short-eared owl (Table 1). Mammals of rabbit size or larger comprised only 0.5% of all prey items analyzed. This accords with the figures for the medium-sized owls. In the larger barred owl, rabbits increase to 6.5%; in the still larger snowy and great-horned owls, from 24% to 46%. They are unrepresented in the diet of smaller species like the screech owl, *Otus asio*.

The candidates most likely to be responsible for the bulk of the deposit are the eared owls (*Asio*, sp.) and the barn owl. The high percentage of field forms in the deposit, primarily voles of the genus *Microtus*, suggests a predator that hunts in open country, like the barn owl and the short-eared owl. Basically the short-eared owl (*A. flammeus*) is an open grassland-roosting bird, while the long-eared owl (*A. otus*) is a pine/brush thicket-roosting species.

Table 1. Diet of various owls from eastern North America.¹

Species	Owl total length	% Rabbit class	% Squirrel class	% Mice class	% All bird	N
<i>Nyctea scandiaca</i> snowy owl	20"	24.0	12.0	20.0	39.0	251
<i>Bubo virginianus</i> great horned owl	20"	46.0	11.0	33.0	17.0	2,714
<i>Strix varia</i> barred owl	17"	6.5	7.0	78.0	8.0	521
<i>Tyto alba</i> barn owl	14"	.1	1.2	95.0	1.4	8,151
<i>Asio otus</i> long-eared owl	13"	.5	.3	94.0	2.4	2,112
<i>Asio flammeus</i> short-eared owl	13"	.3	5.0	93.0	2.0	263
<i>Aegolius funereus</i> boreal owl	10"	—	—	93.0	7.0	15
<i>Otus asio</i> screech owl	8"	—	—	83.0	6.0	73
<i>Aegolius acadicus</i> saw-whet owl	7"	—	—	96.0	4.0	21
owl, ?species Clark's Cave, sample Pleistocene	—	.5	2.8	95.0	2.2	4,562

¹N = Stomach/pellets examined except for Clark's Cave, where it indicates minimum number of animals in fossil prey population. Raw data from Latham, R.M., 1950.



Fig. 9. Mildly xeric shale barren habitat on low shale hills of southern side of Cowpasture River valley. Fig. 10 taken from same spot. Right edge of photo overlaps left edge of Fig. 10.

The barn owl is associated primarily with the Carolinian Life Zone. It occurs no farther north than southern New York State, and avoids the higher portions of the Appalachian Mountains. It does occur at the site today. Both feathers and fresh pellets were picked up along the cliff face by Parmalee in July 1974. The predominantly boreal character of the fossil-prey species, many of which do not occur in the Appalachians today, reflecting the effects of the Wisconsin glacialation, do not appear to be likely barn owl prey, given the present ecological requirements of that species. If the long-eared owl inhabited the cave it could have been responsible for a large portion of the boreal meadow voles in the de-

posit. It is possible, however, that the barn owl, despite its modern temperate range, may have inhabited the cave during the late Pleistocene.

Small egg-shell fragments were distributed randomly throughout the deposit. Dr. Mary H. Clench compared them with modern eggs from the CMNH collections, but they could not be identified with certainty. At least some of the fragments appear to be from birds of large size e.g., eagle or vulture.

In summary, the Clark's Cave fossil deposit represents nest debris of some medium-size owl, or owls, with additions from other raptorial species throughout its long depositional history.

QUANTITATIVE ANALYSIS

All birds and small mammals recovered from the fauna are Recent species, so that the Clark's Cave fossil fauna can be expressed quantitatively by the

cumulative body weights of the 114 species of birds and mammals considered to be raptor prey. The relative contribution to the raptor diet of the various



Fig. 10. Oak (*Quercus*)-forested hills along northern side of Cowpasture River valley, 2 kilometers upstream from Clark's Cave, Bath County, Virginia. Note broad flood plain, probable source of many of the fossil voles from the cave deposit. Cave out of sight around far left hill. River flows along base of forested hills from right to left.

species or species groups represented can be ascertained. Average live weight of individuals of each species considered raptor prey (Faunal List, Table 4) was multiplied by the minimum number of individuals of that species recovered. The resulting cumulative weights had little meaning as far as expressing actual totals consumed or the true relative caloric value of each species in the raptor diet, because of the many variables involved. But when these figures are compared, they give some indication of relative contributions to the raptor diet. Weights were obtained from the literature and represent average approximations. Various authorities did not always agree. Mammal weights were taken from Banfield, 1974, Doult *et al.*, 1973, and Youngman, 1975. Bird weights were furnished by Dr. Kenneth Parkes, who stresses that "average" figures, especially for birds with great sexual weight disparity, like the turkey or sharp-shinned hawk, are rough indeed. Despite the unavoidable crudeness of the analysis, trends emerge

that probably parallel the true picture.

The total estimated biomass represented by the recovered fossils was 277.82 kg, 73.5% (204.31 kg) mammal remains, 26.5% (73.51 kg) birds. Results are summarized in Table 2 by families. Voles (Arvicolidae) contributed most heavily both in terms of individuals (45.2%) and in terms of body weight (36.6%). Although birds accounted for only 4.6% of the combined numbers of individual birds and mammals, grouse (Tetraonidae) accounted for 13.6% of the estimated biomass, ranking second only in importance to the voles.

Bats, ranking second in terms of individual animals recovered (34.0%), contributed only 5.5% to the estimated biomass. Voles, rabbits and hares (Leporidae), and grouse accounted for 63% of the estimated biomass. Other small rodents (Cricetidae, Sciuridae, Zapodidae) comprised an additional 15%. Although there were more species of birds than mammals, they—with the exception of grouse, pigeons (Colum-

idae), and ducks (Anatidae) contributed little to the raptor diet.

In terms of biomass, hares ranked third (Table 2) because of their high individual body weight, but they contributed only 0.5% of the number of individual birds and mammals recovered. Of the 15 most common species, in terms of numbers of individuals recovered from the site (Table 3), not a single bird ranked. Eight species of small rodents, 4 bats, and 2

shrews (12.5% of the 120 species of birds and mammals from the site) accounted for 86% of the 4,555 individuals recovered.

In summary, the deposit was overwhelmingly composed of small rodents and bats, and in terms of individuals, all other species found were present in incidental numbers. But in terms of biomass, voles, grouse, and hares were most important in their contribution to the avian diet.

Table 2. Biomass and minimum numbers of individuals from Clark's Cave.¹

Estimated live weight			Numbers of individuals		
Family	kg	%	Family	Individuals	%
1. Arvicolidae – voles	101.59	36.6	1. Arvicolidae – voles	2,060	45.2
2. Tetraonidae – grouse	37.78	13.6	2. Vespertilionidae – bats	1,554	34.0
3. Leporidae – hares	35.47	12.8	3. Cricetidae – deer mice and wood rats	272	5.9
4. Cricetidae – deer mice and wood rats	23.10	8.3	4. Soricidae – shrews	231	5.0
5. Sciuridae – squirrels	19.93	7.2	5. Sciuridae – squirrels	117	2.5
6. Vespertilionidae – bats	15.22	5.5	6. Tetraonidae – grouse	75	1.6
7. Columbidae – pigeons	9.00	3.2	All others (42 families)	253	5.5
8. Anatidae – ducks	8.54	3.1			
All others (40 families)	27.19	9.7			

¹Avian and mammalian families ranked in order of representation.

Table 3. Fifteen most abundant vertebrates¹ in Clark's Cave.

Species	Individuals	%
1. <i>Myotis lucifugus/sodalis/keenii</i> – little brown bats	c. 877	19.3
2. <i>Microtus pennsylvanicus</i> – meadow vole	c. 658	14.5
3. <i>Microtus xanthognathus</i> – yellow-cheeked vole	511	11.2
4. <i>Eptesicus fuscus</i> – big brown bat	363	8.0
5. <i>Clethrionomys gapperi</i> – red-backed vole	305	6.7
6. <i>Microtus chrotorrhinus</i> – rock vole	c. 292	6.4
7. <i>Microtus pinetorum</i> – woodland vole	170	3.7
8. <i>Myotis leibii</i> – Leib's bat	c. 138	3.0
9. <i>Myotis grisescens</i> – gray bat	c. 138	3.0
10. <i>Peromyscus maniculatus</i> – deer mouse	c. 117	2.6
11. <i>Peromyscus leucopus</i> – white footed mouse	c. 104	2.3
12. <i>Blarina brevicauda</i> – short-tailed shrew	97	2.1
13. <i>Sorex cinereus</i> – masked shrew	67	1.5
14. <i>Synaptomys borealis</i> – northern bog lemming	61	1.3
15. <i>Phenacomys intermedius</i> – heather vole	34	0.1
104 additional species	618	14.3

¹Ranked by numbers of individuals.

Table 4. Plant and animal remains, Entrance 2, Site 3, Clark's Cave.

Scientific name	Common name	MNI	
FLORA¹			
(Identified by F. Brunett)			
1. <i>Tsuga cf. canadensis</i>	hemlock	—	needles
2. <i>Thuja occidentalis</i>	arbor vitae	—	branchlets, seeds
3. <i>Carya</i> , ?species	hickory	—	nut fragment
4. <i>Quercus</i> , ?species	oak	—	acorn fragment
5. <i>Celtis occidentalis</i>	hackberry	c. 150	seeds
6. <i>Phytolacca decandra</i>	pokeweed	c. 35	seeds
7. <i>Vitis</i> , ?species	grape	12	seeds
8. <i>Nyssa sylvatica</i>	black gum	9	seeds
CRUSTACEA			
(Identified by H.H. Hobbs, Jr.)			
1. <i>Cambarus cf. bartonii</i>	crayfish	4	
2. <i>Cambarus cf. longulus</i>	crayfish	2	
INSECTA¹			
(Identified by E.D. Cashatt)			
1. <i>Dicaelus</i> , ?species	Carabid (ground) beetle	1	
2. <i>Galerita cf. bicolor</i>	Carabid (ground) beetle	1	
3. <i>Calasoma</i> , ?species	Carabid (ground) beetle	2	
Carabidae, ?species	Carabid (ground) beetle	9	
4. <i>Onthophagus cf. janus</i>	scarab beetle	5	
<i>Onthophagus</i> , ?species	scarab beetle	1	
5. <i>Canthon</i> , ?species	scarab beetle	1	
6. <i>Balbocerosoma</i> , ?species	scarab beetle	1	
7. <i>Trox</i> , ?species	trogid (hide) beetle	1	
8. Elateridae, ?species	elaterid (click) beetle	1	
Coleoptera, ?species	beetles, unidentified	6	
9. Membracidae, ?species	leafhopper	1	
10. Calliphoridae or Sarcophagidae	fleshflies	pupae	
11. Vespidae, ?species	social wasps	2	
GASTROPODA¹			
	Snails	4,363	
(Identified by L. Hubricht and W.J. Clench)			
1. <i>Hendersonia occulta</i>	land snail	2	
2. <i>Vallonia costata</i>	land snail	5	
3. <i>Gastrocopta armifera</i>	land snail	1	
4. <i>Gastropoda contracta</i>	land snail	1	
5. <i>Vertigo tridentata</i>	land snail	3	
6. <i>Vertigo gouldi</i>	land snail	3	
7. <i>Columella simplex</i>	land snail	1	
8. <i>Catinella</i> , ?species	land snail	1	
9. <i>Anguispira alternata</i>	land snail	5	
10. <i>Discus catskillensis</i>	land snail	7	

¹Not considered owl prey.

Table 4. Plant and animal remains, Entrance 2, Site 3, Clark's Cave (continued).

Scientific name	Common name	MNI
GASTROPODA (continued)		
11. <i>Helicodiscus parallelus</i>	land snail	12
12. <i>Helicodiscus inermis</i>	land snail	2
13. <i>Helicodiscus jacksoni</i>	land snail	2
14. <i>Stenotrema hirsutum</i>	land snail	3
15. <i>Stenotrema fraternum</i>	land snail	1
16. <i>Triodopsis burchi</i>	land snail	1
17. <i>Triodopsis vulgata</i>	land snail	1
18. <i>Triodopsis juxtidentis</i>	land snail	5
19. <i>Strobilops labyrinthica</i>	land snail	7
20. <i>Spirodon carinata</i>	freshwater snail	c. 4,300
BIVALVIA ¹	Clams	140
(Identified by W.J. Clench)		
1. <i>Sphaerium striatinum</i>	finger nail clam	1
2. <i>Pisidium dubium</i>	finger nail clam	139
OSTEICHTHYS	Bony fishes	57
(Identified by J.E. Guilday)		
1. <i>Anguilla</i> cf. <i>bostoniensis</i>	American eel	1
2. <i>Esox</i> cf. <i>americanus</i> or <i>niger</i>	pickerel	1
3. <i>Semotilus</i> cf. <i>corporalis</i>	creek chub	26
4. <i>Nocomis</i> cf. <i>raneyi</i>	river chub	
Cyprinidae, unidentified	unidentified minnows	
5. <i>Catostomus</i> , ?species	white sucker	18
6. <i>Moxostoma</i> , ?species	redhorse sucker	
Catostomidae, unidentified	sucker	
7. <i>Noturus</i> , ?species	stonecat	11
Ictaluridae, unidentified	small catfish	
AMPHIBIA	Frogs, toads, salamanders	328
(Identified by H. McGinnis)		
1. <i>Bufo</i> (<i>americanus</i> group)	toad	141
2. <i>Hyla</i> cf. <i>crucifer</i>	peeper	20
3. <i>Rana</i> cf. <i>catesbiana</i>	bullfrog	5
4. <i>Rana</i> cf. <i>clamitans</i>	green frog	2
5. <i>Rana</i> cf. <i>pipiens</i>	leopard frog	22
6. <i>Rana</i> cf. <i>palustris</i>	pickerel frog	22
7. <i>Rana</i> cf. <i>sylvatica</i>	wood frog	42
<i>Rana</i> , unidentified	frog	38
8. <i>Ambystoma</i> , ?species	mole salamander	c. 4
9. Plethodontidae or Salamandridae	salamander	c. 32
REPTILIA	Reptiles	37
(Identified by J.E. Guilday)		
1. cf. Testudinidae	turtle	1

Table 4. Plant and animal remains, Entrance 2, Site 3, Clark's Cave (continued).

Scientific name	Common name	MNI		
REPTILIA (continued)				
2. <i>Sceloporus</i> cf. <i>undulatus</i>	fence lizard	13		
3. <i>Eumeces</i> cf. <i>laticeps</i>	broadheaded skink	2		
4. Colubridae, ?species	non-poisonous snake	c. 20		
5. Crotalidae, ?species	rattlesnake or copperhead	1		
			Gram live weight	Total gram live weight
AVES				
	Birds	219		
(Identified by P.W. Parmalee)				
1. <i>Podilymbus podiceps</i>	pied-billed grebe	2	135	270
2. <i>Botaurus lentiginosus</i>	American bittern	1	475	475
3. <i>Anas</i> cf. <i>platyrhynchos</i> or <i>rubripes</i>	mallard or black duck	2	1,160	2,320
4. cf. <i>Anas crecca</i>	green-winged teal	1	350	350
5. cf. <i>Anas discors</i>	blue-winged teal	1	400	400
6. <i>Lophodytes cucullatus</i>	hooded merganser	2	610	1,220
7. <i>Mergus</i> , ?species	merganser	1	c. 750	c. 750
Anatidae, ?species	ducks, unidentified	5	c. 700	c. 3,500
8. <i>Accipiter striatus</i>	sharp-shinned hawk	1	135	135
9. <i>Buteo</i> cf. <i>platypterus</i>	broad-winged hawk	1	400	400
Accipitridae, ?species	hawks, unidentified	2	c. 575	c. 1,150
10. <i>Falco sparverius</i>	American kestrel	2	115	230
11. cf. <i>Canachites canadensis</i>	spruce grouse	14	470	6,580
12. <i>Bonasa umbellus</i>	ruffed grouse	16	510	8,160
<i>C. canadensis</i> or <i>B. umbellus</i>	spruce or ruffed grouse	c. 30-35	c. 490	17,150
13. <i>Lagopus</i> cf. <i>mutus</i>	rock ptarmigan	1	450	450
14. cf. <i>Pedioecetes phasianellus</i>	sharp-tailed grouse	3	735	2,205
Tetraonidae, ?species	grouse, unidentified	6	c. 540	c. 3,240
15. <i>Colinus virginianus</i>	bobwhite	2	165	330
16. <i>Meleagris gallopavo</i>	wild turkey	1	5,450	5,450
17. cf. <i>Rallus limicola</i>	Virginia rail	1	85	85
18. <i>Porzana carolina</i>	sora rail	2	80	160
19. <i>Gallinula chloropus</i>	common gallinule	1	600	600
Rallidae, ?species	rail, unidentified	1	c. 83	c. 83
20. <i>Pluvialis dominica</i>	American golden plover	1	145	145
21. <i>Philohela minor</i>	American woodcock	4	155	620
22. <i>Capella gallinago</i>	common snipe	1	100	100
23. cf. <i>Actitis macularia</i>	spotted sandpiper	2	40	80
24. cf. <i>Tringa solitaria</i>	solitary sandpiper	2	60	120
25. cf. <i>Limosa</i> , ?species	godwit	3	350	1,050
Scolopacidae, ?species	sandpiper/plover	7	c. 75	c. 525
26. <i>Ectopistes migratorius</i>	passenger pigeon	30	300	9,000
27. <i>Coccyzus</i> , ?species	cuckoo	1	60	60
28. <i>Otus asio</i>	screech owl	1	160	160
29. <i>Bubo virginianus</i>	great horned owl	1	1,375	1,375

Table 4. Plant and animal remains, Entrance 2, Site 3, Clark's Cave (continued).

Scientific name	Common name	MNI	Gram live weight	Total gram live weight
AVES (continued)				
30. <i>Asio</i> cf. <i>flammeus</i> or <i>otus</i>	short-eared or long-eared owl	3	400	1,200
31. <i>Aegolius acadicus</i>	saw-whet owl	1	85	85
32. <i>Chordeiles minor</i>	common nighthawk	1	80	80
33. <i>Chaetura pelagica</i>	chimney swift	1	22	22
34. <i>Megaceryle alcyon</i>	belted kingfisher	1	140	140
35. <i>Colaptes auratus</i>	common flicker	3	135	405
36. <i>Dryocopus pileatus</i>	pileated woodpecker	2	280	560
37. cf. <i>Centurus carolinus</i>	red-bellied woodpecker	1	78	78
38. <i>Sphyrapicus varius</i>	yellow-bellied sapsucker	1	50	50
39. <i>Dendrocopos villosus</i>	hairy woodpecker	1	50	50
40. <i>Dendrocopos pubescens</i>	downy woodpecker	1	26	26
Picidae, ?species	woodpeckers, unidentified	2	c. 70	c. 140
41. <i>Empidonax</i> , ?species	flycatcher	1	c. 12	c. 12
42. <i>Eremophila alpestris</i>	horned lark	1	40	40
43. <i>Petrochelidon pyrrhonota</i>	cliff swallow	9	23	207
44. <i>Perisoreus canadensis</i>	gray jay	1	75	75
45. cf. <i>Cyanocitta cristata</i>	blue jay	1	85	85
46. <i>Corvus brachyrhynchos</i>	common crow	1	412	412
47. <i>Parus</i> , ?species	chickadee	1	10	10
48. <i>Parus bicolor</i>	tufted titmouse	1	21	21
49. <i>Sitta</i> cf. <i>canadensis</i>	red-breasted nuthatch?	1	11	11
50. <i>Certhia familiaris</i>	brown creeper	2	8	16
51. <i>Cistothorus</i> cf. <i>platensis</i>	short-billed marsh wren?	1	9	9
52. cf. <i>Toxostoma rufum</i>	brown thrasher	1	70	70
53. <i>Turdus migratorius</i>	robin	2	80	160
54. <i>Catharus</i> , ?species	thrush	2	c. 32	c. 64
55. cf. <i>Sialia sialis</i>	eastern bluebird	1	31	31
56. cf. <i>Anthus spinoletta</i>	water pipit	1	23	23
57. <i>Bombycilla cedrorum</i>	cedar waxwing	1	31	31
58. cf. <i>Dendroica coronata</i>	yellow-rumped warbler	1	13	13
59. <i>Seiurus</i> , ?species	water thrush	1	20	20
Parulidae, ?species	warblers, unidentified	2	c. 12	c. 24
60. cf. <i>Dolichonyx oryzivorus</i>	bobolink	1	34	34
61. cf. <i>Sturnella</i> , ?species	meadowlark	1	97	97
62. <i>Agelaius phoeniceus</i>	red-winged blackbird	1	60	60
63. cf. <i>Icterus spurius</i>	orchard oriole	1	21	21
64. <i>Piranga</i> , ?species	tanager	1	29	29
65. cf. <i>Pinicola enucleator</i>	pine grosbeak	1	57	57
66. <i>Loxia</i> , ?species	crossbill	1	30	30
67. <i>Pooecetes gramineus</i>	vesper sparrow	1	25	25
68. <i>Junco hyemalis</i>	dark-eyed junco	2	20	40
Fringillidae, ?species	sparrows, unidentified	2	c. 18	c. 36

Table 4. Plant and animal remains, Entrance 2, Site 3, Clark's Cave (continued).

Scientific name	Common name	MNI	Gram live weight	Total gram live weight
MAMMALIA	Mammals	4,343		204,315.0
(Identified by J.E. Guilday)				
1. <i>Sorex arcticus</i>	arctic shrew	13	8.3	107.9
2. <i>Sorex cinereus</i>	masked shrew	67	4.1	274.7
3. <i>Sorex dispar</i>	long-tailed shrew	4	5.0	20.0
4. <i>Sorex fumeus</i>	smoky shrew	10	8.0	80.0
5. <i>Sorex palustris</i>	water shrew	7	12.3	86.1
<i>Sorex</i> , ?species	shrews, unidentified	26	c. 7.5	c. 196.0
6. <i>Microsorex hoyi</i>	pygmy shrew	7	3.2	22.4
7. <i>Blarina brevicauda</i>	short-tailed shrew	97	19.3	1,872.1
8. <i>Parascalops breweri</i>	hairy-tailed mole	12	52.0	624.0
9. <i>Scalopus aquaticus</i>	eastern mole	1	102.0	102.0
10. <i>Condylura cristata</i>	star-nosed mole	13	56.5	734.5
11. <i>Myotis lucifugus</i> or <i>sodalis</i>	little brown bat	c. 877	c. 7.5	c. 8,647.0
12. <i>Myotis keenii</i>	Keen's bat			
13. <i>Myotis leibii</i>	small-footed bat	c. 138		
14. <i>Myotis grisescens</i>	gray bat	c. 138		
15. <i>Pipistrellus subflavus</i>	eastern pipistrelle	26	4.5	117.0
16. <i>Eptesicus fuscus</i>	big brown bat	363	17.5	6,352.5
17. <i>Plecotus</i> cf. <i>townsendii</i>	big-eared bat	9	7.5	67.5
18. <i>Lasiurus borealis</i>	red bat	3	12.0	36.0
19. cf. <i>Sylvilagus transitionalis</i>	New England cottontail	1	969.0	969.0
20. <i>Lepus americanus</i>	snowshoe hare	23	1,500.0	34,500.0
21. <i>Tamias striatus</i>	eastern chipmunk	24	97.0	2,328.0
22. <i>Eutamias minimus</i>	least chipmunk	3	42.9	128.7
23. <i>Marmota monax</i>	woodchuck	2	2,850.0	5,700.0
24. <i>Spermophilus tridecemlineatus</i>	13-lined ground squirrel	5	150.0	750.0
25. <i>Sciurus</i> cf. <i>carolinensis</i>	gray squirrel	3	520.0	1,560.0
26. <i>Tamiasciurus hudsonicus</i>	red squirrel	25	185.0	4,625.0
27. <i>Glaucomys volans</i>	southern flying squirrel	19	60.0	1,140.0
28. <i>Glaucomys sabrinus</i>	northern flying squirrel	28	107.0	2,996.0
<i>Tamias</i> or <i>Glaucomys</i>	squirrels, unidentified	8	c. 88.0	c. 704.0
29. <i>Peromyscus maniculatus</i>	deer mouse	c. 117	21.0	c. 2,457.0
30. <i>Peromyscus leucopus</i>	white-footed mouse	c. 104	22.0	c. 2,288.0
31. <i>Neotoma floridana</i>	eastern woodrat	51	360.0	18,360.0
32. <i>Clethrionomys gapperi</i>	red-backed vole	305	24.0	7,320.0
33. <i>Phenacomys intermedius</i>	heather vole	34	33.0	1,122.0
34. <i>Microtus pennsylvanicus</i>	meadow vole	c. 658	35.9	23,622.0
35. <i>Microtus chrotorrhinus</i>	rock vole	c. 292	35.0	10,220.0
36. <i>Microtus xanthognathus</i>	yellow-cheeked vole	511	90.0	45,990.0
37. <i>Microtus pinetorum</i>	woodland vole	170	25.6	4,352.0
38. <i>Ondatra zibethicus</i>	muskrat	6	1,050.0	6,300.0
39. <i>Synaptomys cooperi</i>	southern bog lemming	23	28.3	650.9
40. <i>Synaptomys borealis</i>	northern bog lemming	61	33.0	2,013.0

Table 4. Plant and animal remains, Entrance 2, Site 3, Clark's Cave (continued).

Scientific name	Common name	MNI	Gram live weight	Total gram live weight
MAMMALIA (continued)				
41. <i>Zapus hudsonius</i>	meadow jumping mouse	22	18.0	396.0
42. <i>Napaeozapus insignis</i>	woodland jumping mouse	15	24.0	360.0
43. <i>Erethizon dorsatum</i>	porcupine	1	*	*
44. <i>Canis cf. dirus</i>	dire wolf	1	*	*
45. <i>Ursus americanus</i>	black bear	1	*	*
46. <i>Procyon lotor</i>	raccoon	1	*	*
47. <i>Martes americana</i>	marten	1	661.0	661.0
48. <i>Mustela nivalis</i>	least weasel	7	41.0	287.0
49. <i>Mustela erminea</i>	ermine	4	54.0	216.0
<i>Mustela, (frenata or erminea)</i>	weasel, unidentified	1	c. 60.0	c. 60.0
50. <i>Mustela vison</i>	mink	2	620.0	1,240.0
51. <i>Mephitis mephitis</i>	striped skunk	1	1,660.0	1,660.0
52. <i>Cervus elaphus</i>	elk	1	*	*
53. cf. <i>Odocoileus virginianus</i>	white-tailed deer	1	*	*

BIOTIC DISCUSSIONS

FLORA

Plant remains, probably of Recent origin, were incidental in the deposit. Some (hackberry seeds) were probably introduced by cliff-frequenting rodents, others (hemlock needles, etc.), by wind. All eight species grow in the area today. (Floral List, Table 4).

DECAPODA—Crayfish

The few crayfish represented were probably raptor food remains. Two species, represented by claw fragments, were present. *Cambarus cf. bartonii* and *C. cf. longulus* are both present in the Cowpasture River today. The former ranges from Georgia north to New Brunswick, the latter from the Yadkin River of North Carolina to the James River drainage. Dr. Hobbs comments "The punctations on the fingers are somewhat larger than those typical of either species, but if these remains had passed through the alimentary canal of some mammal [or bird, ed.] this may have been responsible for the disproportionately greater solution of these setae-bearing depressions" (letter, 3/7/73).

INSECTA—Insects

Insect remains were scarce and fragmentary. Twenty-nine of the 32 individuals identified were beetles. Scarab beetles, hide beetles, and flesh flies are attracted to decaying organic matter like raptor roost litter. Wasps probably used the cliffs as nest sites protected from the weather. All remains appeared to be Recent.

MOLLUSCA—Snails and Clams

Approximately 4,363 gastropods were recovered, some 4,300 of which were the small freshwater snail *Spirodon carinata*, common in the river today. They may have formed a minor food item or been inadvertently introduced clinging to nesting materials collected by birds or woodrats. Nineteen species of land snails were represented by only 63 shells in this seemingly lime-rich environment. The site may have been too dry or the decaying owl pellets too acidic to attract them. All species are still present in the area and are broadly distributed in the Appalachians today.

The two species of fingernail clams (Sphaeriidae) were probably also inadvertent inclusions.

PISCES—Fish

Remains of 57 small fish, seven species, 1% of the total vertebrates, were recovered. They were uniformly small and minnow-size, although a few of the suckers reached an estimated length of 30 cm. Identifications were based upon diagnostic cranial elements, and in the case of catfish, pectoral fin spines as well. Approximately 4,000 unidentified small fish vertebrae were recovered. All identified species are present in the James River drainage today. The fish are catalogued under CM 29689.

Fish formed a minor food item and may have been taken by bankside scavenging or inadvertently introduced as stomach contents of other prey items. But at least some owls do actively fish. Dr. Claude W. Hibbard (letter, 10/15/62) reported finding, as a boy, screech owls (*Otus asio*) caught in jump traps set in shallow water that had been baited with shiny tin-foil to attract curious raccoons. The owls apparently mistook the shiny foil for fish and struck.

AMPHIBIA—Amphibians

Order Anura—Frogs and Toads

Family Bufonidae

Bufo (*americanus* group, *sensu* Blair)—Toad

MATERIAL: CM 29582: 141 left, 133 right ilia. MNI = 141 individuals.

Family Hylidae

Hyla cf. *crucifer*—Spring Peeper

MATERIAL: CM 29581: 20 left, 17 right ilia. MNI = 20 individuals.

Family Ranidae

Rana cf. *catesbeiana*—Bullfrog

MATERIAL: CM 29574: 5 left, 2 right ilia. MNI = 5 individuals.

Rana cf. *clamitans*—Green Frog

MATERIAL: CM 29575: 1 left, 2 right ilia. MNI = 2 individuals.
CM 29576: (*R. catesbeiana* or *clamitans*): 2 left, 2 right ilia. MNI = 2 individuals.

Rana cf. *pipiens* group—Leopard Frog

MATERIAL: CM 29577: 13 left, 22 right ilia. MNI = 22 individuals.

Rana cf. *palustris*—Pickerel Frog

MATERIAL: CM 29578: 18 left, 22 right ilia. MNI = 22 individuals.

Rana cf. *sylvatica*—Wood Frog

MATERIAL: CM 29579: 41 left, 42 right ilia. MNI = 42 individuals.

Rana, species indeterminate

MATERIAL: CM 29580: 36 left, 29 right fragmentary ilia. MNI = 36 individuals.

REMARKS: A minimum of 141 toads and 151 frogs, 6% of the total vertebrates, were recovered from the site. Identifications were based primarily on characters of the ilium, although frontoparietals and sacra were also studied. The following ilial characters were used:

Rana catesbeiana: steep posterior slope of ilial prominence, non-sinuate outline of the prominence viewed dorsally; large size.

R. clamitans: steep posterior slope of ilial prominence; sinuate outline of the prominence viewed dorsally (except in immature specimens).

R. pipiens: moderately steep angle of ilial prominence; presence of a ridge and pit; ilial prominence blade-like to moderately knob-like (may be some overlap with *R. sylvatica*).

R. palustris: gently sloping ilial prominence and well-defined ridge (Holman, 1967). Some specimens could be *R. pipiens* or *R. sylvatica*.

Hyla crucifer: The hylid ilia from Clark's Cave are referable to *Hyla* on the basis of the ventral acetabular expansion, which is wider than in *Acris* or *Pseudacris*. The angle between the shaft of the ilium and the acetabular expansion is obtuse, unlike *Acris* and *Pseudacris*. *Hyla crucifer* is unusual for the genus in that dorsal protuberance is almost always above the anterior half of the acetabular fossa, or completely anterior to it (Lynch, 1966). This is the case in all Clark's Cave specimens.

Considering the boreal nature of the deposit, the possibility of mink frog, *R. septentrionalis* was considered. Thirteen of the 237 *Rana* ilia had a keel on the shaft, a character noted on three Recent specimens of the mink frog from the Carnegie Museum collections. These also lacked a pit. However, all of the Clark's Cave specimens may be variants of *R. pipiens*, *R. palustris*, or *R. sylvatica*.

The peepers, *H. crucifer*, 20 individuals, are arboreal, small, and probably not available for predation by raptors except perhaps during spring breeding aggregation. Their occurrence at the site is incidental.

Of the remaining 131 frogs, 5 species of the genus *Rana*, only 7%, were "deep-water" frogs (river, lake, pond), bull, and green frogs. The other three species, leopard, pickerel, and wood frog, especially the latter, are more terrestrial, frequenting swampland, wet meadows, and woodland. All congregate in standing water swampland during spring breeding aggregation. All are common in the area today. The pickerel frog appears to be especially common in and around

cave streams in Virginia today (Holsinger, 1964).

Birds of prey, like most carnivores, are opportunists, and these frogs were probably prey items. The relatively small number suggests that they were taken sporadically. But frogs would be available only during the warmer portion of the year, so that their relatively low numbers may be a poor reflection of their possible seasonal importance.

Almost one-half of the anurans were toads of the genus *Bufo*. Two species occur in western Virginia at the present time, *Bufo americanus*, the American toad, and *Bufo woodhousei fowleri*, Fowler's toad. The two species could not be separated on the basis of the recovered fossils and both may be represented.

Although remains of the eastern spadefoot toad, *Scaphiopus holbrooki*, were recovered from the Natural Chimneys, Va. deposit, no evidence of this species was noted at Clark's Cave. Nocturnal, terrestrial and slow-moving, toads would appear to be susceptible to owl predation. Frogs and "amphibians" have been reported from owl food remains (Latham, 1950), but toads are rarely specified. Howell, 1932, and Munro, 1929, refer to toads in the stomachs of burrowing owls, *Speotyto cunicularia*, so that the skin secretions, so distasteful to mammals, apparently do not deter at least the burrowing owl. We would like to thank Harold D. Mahan, Director, Cleveland Museum of Natural History, for the bur-

Table 5. Measurements (in mm)¹ of *Bufo* (*americanus* group) Sacra.

Locality	\bar{X}	OR	N
Width of centrum at condyles			
Clark's Cave, Va., late Pleistocene	28.89	22.5–36.0	33
New Paris No. 4, Pa., late Pleistocene	-----	11.5–32.5	---
Southwestern Pa., Recent CM 37153, <i>Bufo americanus</i>	34.5	-----	1
Length of centrum			
Clark's Cave, Va., late Pleistocene	25.34	20.0–34.5	32
New Paris No. 4, Pa., late Pleistocene	-----	11.5–31.0	---
Southwestern Pa., Recent CM 37153, <i>Bufo americanus</i>	33.0	-----	1
Width of centrum, anterior end			
Clark's Cave, Va., late Pleistocene	22.0	16.0–33.0	31
New Paris No. 4, Pa., Southwestern Pa., Recent	-----	10.0–23.5	---
CM 37153, <i>Bufo americanus</i>	28.0	-----	1
Height of centrum, anterior end			
Clark's Cave, Va., late Pleistocene	14.1	9.0–17.5	33
New Paris No. 4, Pa., late Pleistocene	-----	6.0–15.0	---
Southwestern Pennsylvania, Recent CM 37153, <i>Bufo americanus</i>	15.0	-----	1

¹Measurements by H. McGinnis.

rowing owl observations.

Measurements of *Bufo sacra* from Clark's Cave appear to fall within the range of Recent *Bufo americanus*, and are larger than those of the smaller of the two size groups from New Paris No. 4, Pa., identified as *B. a. copei*.

Order Urodela—Salamanders

A minimum of 36 salamanders, estimated by vertebra and limb bone counts, are catalogued under CM 29692 (see Faunal List). They were undoubtedly incidental food items. Although salamanders are common in the area, the immediate excavation site appears too well-drained and dry to attract them today.

REPTILIA—Reptiles

Order Chelonia—Turtle

A single unidentified carapace fragment (CM 29695) is the only evidence of turtle in the deposit. Because of the selection bias of the birds of prey it is not clear whether the absence of turtles from the site is a reflection of cooler environmental conditions (as at New Paris No. 4, Pa.) or immunity from predation.

Order Squamata—Lizards and Snakes

A minimum number of 13 fence lizards (CM 29584) and two broad-headed skinks (CM 29585) were based on characters of the dentary and compared directly with Recent specimens from the Carnegie Museum collections. Both species occur at the site today. The fence lizard, also reported from the Natural Chimneys, Va. deposit, reaches its northern limits today in central Pennsylvania, slightly north of the range of the broad-headed skink. Lizard remains probably post-dated the primary boreal deposit.

Snakes, ca 2,800 vertebrae (CM 29693, 29694), an estimated 20+ individuals, accounted for only 0.4% of the total vertebrate MNI. One partial vertebra was from a medium-sized crotalid. All others were from colubrids of small size. Snakes were a minor item of owl diet. Large snakes appear to have been deliberately avoided. Colubrids, especially natricines, were common in the boreal New Paris No. 4 deposit, so those at Clark's Cave may have been contemporaneous with the bulk of the late Pleistocene fauna at the site.

AVES—Birds

Bird remains from the Clark's Cave deposit totaled 3,600 pieces. Approximately 212 individuals, belong-

ing to 68 species in 34 families, were represented. In addition, slightly over 700, or 72% of the bird-bone sample identified to order, consisted of indeterminate passerines. Avian remains from Back Creek Cave No. 2 consisted of 415 pieces, at least 17 species belonging to nine families, a minimum of 55 individuals.

The bulk of the remains resulted from the feeding activities of predatory birds. Such bone concentrations provide an index to the relative abundance and variety of a faunal assemblage, but the condition of the individual bones is often adversely affected by feeding breakage, the effects of digestive fluids, post-depositional breakage and rodent damage. A large percentage of the bones are fragmented and the diagnostic characters of the articulating ends of many are missing. In the case of the avian material from these two cave deposits, it was apparent that the larger the species (e.g. waterfowl, grouse, turkey), the greater the extent of bone fragmentation. This, combined with the difficulty of distinguishing between elements of closely related species, made many identifications only tentative. Factors that prevented species identification, or osteological characters that made certain critical determinations possible, will be discussed under the various families or species of birds below.

Order: Podicipediformes

Family: Podicipedidae—Grebes

Podilymbus podiceps (Linnaeus)—Pied-billed Grebe

MATERIAL: CM 29613. Paired quadrates: incomplete sternum, coracoids, tarsometatarsus, ulna. MNI = 2 individuals.

REMARKS: The pied-billed grebe is a common migrant and fairly common winter resident in the state, occurring on both lakes and rivers. Although all elements (except the quadrates) were incomplete, they are in all probability referable to this species.

Order: Ciconiiformes

Family: Ardeidae—Hérons and Bitterns

Botaurus lentiginosus (Rackett)—American Bittern

MATERIAL: CM 29631. Incomplete left humerus. MNI = 1 individual.

REMARKS: Both ends of this humerus were missing, but the overall dimensions, location of the deltoid crest, and form/position of the impression of the *brachialis anticus* muscle compare favorably with that of the American bittern. Probably an uncommon migrant and summer resident in western Virginia.

Order: Anseriformes

Family: Anatidae—Swans, Geese, and Ducks

Anas platyrhynchos Linnaeus—Mallard, and
Anas rubripes Brewster—Black Duck—or both

MATERIAL: CM 29614. 2 incomplete right humeri. MNI = 2 individuals.

Anas Linnaeus—Duck

MATERIAL: CM 29615. Distal ends of right tibiotarsus and coracoid. MNI = 1 individual.

cf. *Anas crecca* Linnaeus—Green-winged Teal

MATERIAL: CM 29616. Proximal end of left humerus. MNI = 1 individual.

cf. *Anas discors* Linnaeus—Blue-winged Teal

MATERIAL: CM 29617. Incomplete left humerus. MNI = 1 individual.

Lophodytes cucullatus (Linnaeus)—Hooded
Merganser

MATERIAL: CM 29618. 1 proximal end, 1 distal end and shaft of right humeri. MNI = 2 individuals.

Mergus Linnaeus—Merganser

MATERIAL: CM 29678. Incomplete proximal end of left humerus. MNI = 1 individual.

Duck/Merganser spp.

MATERIAL: CM 29619. 23 non-diagnostic or fragmentary elements including coracoids, ulnae, femora, tibiotarsi, humeri.

REMARKS: All waterfowl elements were incomplete, making specific determinations especially tenuous. One indeterminate duck tibiotarsus and sternum and two humeri fragments (CM 29619) were those of small species, possibly teal, while several other pieces probably represent mergansers, some of the larger puddle ducks (*Anas*) or both. All waterfowl species represented at Clark's Cave could be found today along the Cowpasture River, primarily during migration. Because of the large size of mallards, the black duck, and mergansers (*Mergus*), it would have taken a raptor the size of a large hawk (*Buteo*) or great horned owl (*Bubo*) to capture and transport these birds to the cave entrance.

Order: Falconiformes

Family: Accipitridae—Hawks and Harriers

cf. *Accipiter striatus* Vieillot—Sharp-shinned Hawk

MATERIAL: CM 29620. Incomplete right coracoid. MNI = 1 individual.

Buteo platypterus (Vieillot)—Broad-winged Hawk

MATERIAL: CM 29621. Fragmented distal end of right tibiotarsus. MNI = 1 individual.

Hawk sp.

MATERIAL: CM 29622. Claw.

REMARKS: Hawks were poorly represented at Clark's Cave, and the paucity of their remains possibly suggests that the cave entrance was not generally used as a roosting/feeding locale. The tibiotarsus fragment, little more than the tendinal bridge and lacking the condyles, is suggested as being that of broad-winged hawk, based on existing proportions. The claw was from a large hawk the size of a red-tailed hawk. Murray (1952:40) considers the sharp-shinned hawk a fairly common resident in the Lexington area, but an uncommon resident in southwestern Virginia. This small "bird hawk" may have been a major contributor of the numerous passerines in the deposit.

Family: Falconidae Caracaras and Falcons

Falco sparverius Linnaeus—American Kestrel

MATERIAL: CM 29623. 1 complete and 1 proximal half of left carpometacarpal; 1 proximal and 1 distal section of right tarsometatarsal. MNI = 2 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29700. Incomplete left carpometacarpus. MNI = 1 individual.

REMARKS: This small falcon, a fairly common resident or migrant in Virginia, preys upon insects, small birds and mammals. If this raptor frequented the cave entrances, it could have also been a significant contributor of small animals to the deposits.

Order: Galliformes

Family: Tetraonidae—Grouse and Ptarmigan

cf. *Canachites canadensis* (Linnaeus)—Spruce Grouse

MATERIAL: CM 29624. 14 carpometacarpals, 23 tarsometatarsi, 2 humeri, 2 ulnae, 1 coracoid, 4 tibiotarsi. MNI = 14 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29701. 10 tarsometatarsi. MNI = 6 individuals.

Bonasa umbellus (Linnaeus)—Ruffed Grouse

MATERIAL: CM 29625. Complete (or sections of) items including 1 jaw, 1 femur, 4 coracoids, 2 tibiotarsi; 24 tarsometatarsi, 14 humeri, 3 ulnae, 26 carpometacarpals. MNI = 16 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29702. 8 carpometacarpals, 10 tarsometatarsi. MNI = 6 individuals.

C. canadensis and/or *B. umbellus*—
Spruce or Ruffed Grouse, or both

MATERIAL: CM 29626. A total of approximately 272 incomplete, fragmented, or non-diagnostic elements. MNI—30 to 35 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29703. A total of approximately 80 incomplete, fragmented, or non-diagnostic elements. MNI = 9 individuals.

REMARKS: Osteological differences between spruce and ruffed grouse are extremely subtle and, taking into account overlap in size between males and females within and between the species, the majority of elements of these two grouse are specifically inseparable. In general, however, certain bones of the spruce grouse appear slightly more delicate (comparing birds of the same sex) than those of the ruffed grouse. For example, the tarsometatarsus of the spruce grouse is shorter and the shaft narrower or "pinched" just posterior to the distal foramen. The pneumatic foramen in the spruce grouse humerus appears proportionally larger and more rounded (oval in *Bonasa*). The carpometacarpus of the ruffed grouse appears heavier or stouter compared with one of equal length from the spruce grouse, and the intermetacarpal process in ruffed grouse appeared better developed in the comparative specimens examined. While species identification based on other bones are more tentative it is felt that these deter-

minations are valid and that the spruce grouse as well as the ruffed grouse is represented at both caves.

The ruffed grouse is still common in the more heavily forested regions of western Virginia. The spruce grouse, on the other hand, "a bird of the northern wilderness, of thick and tangled swamps, and of spruce forests, where the ground is deep in moss and where the delicate vines of the snowberry and twinflower clamber over moss-covered stubs and fallen, long-decayed tree trunks" (Bent, 1932: 121), was unknown in the state in historic times. Wetmore (1959) identified remains of *C. canadensis* from Natural Chimneys, Va. With the added records of this bird from the two Bath Co. caves, it is apparent that at one time this boreal grouse was definitely a part of the avifauna of western Virginia. It has also been reported from the late Pleistocene Ladds Quarry local fauna, Bartow Co., Ga. (Wetmore, 1967).

Lagopus cf. mutus (Montin)—Rock Ptarmigan

MATERIAL: CM 29627. Complete left humerus and tarsometatarsus. MNI = 1 individual.

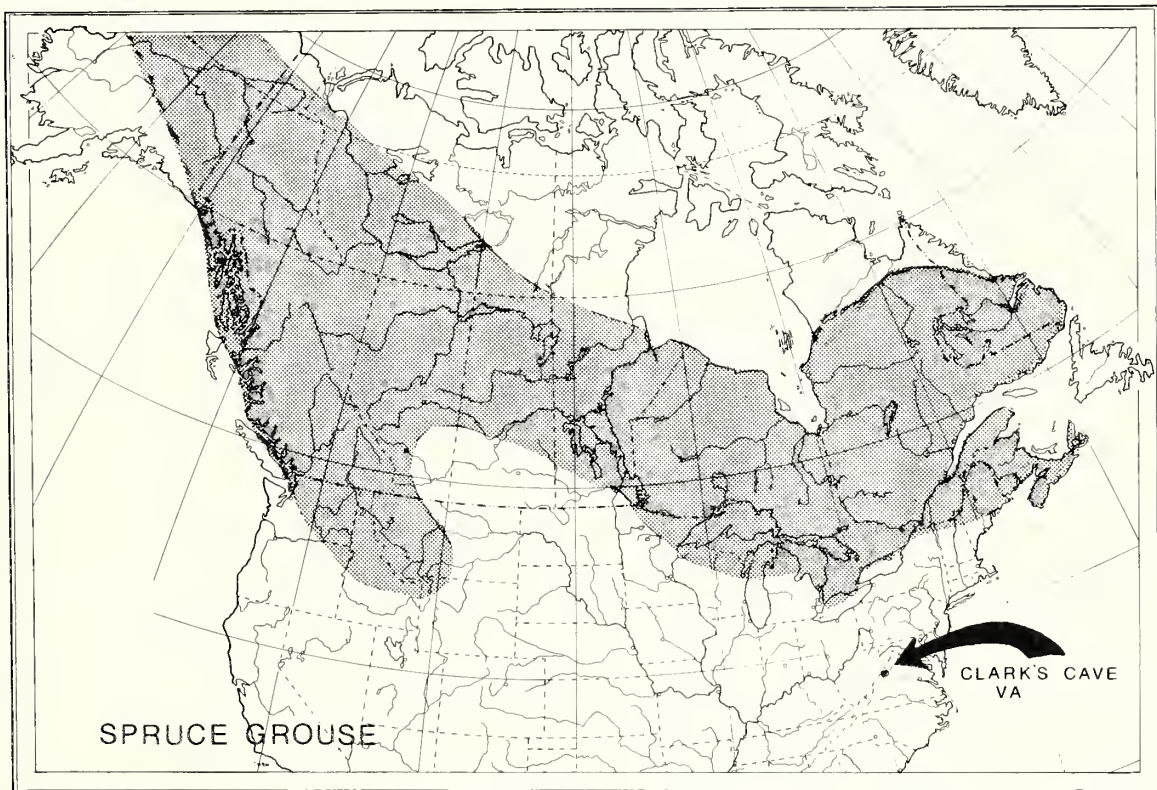


Fig. 11. Modern range of spruce grouse, *Canachites canadensis* (Linnaeus), adapted from Godfrey, 1966. Present in Clark's Cave local fauna.

MATERIAL (Back Creek Cave No. 2): CM 29704. 1 complete right and 2 left tarsometatarsi. MNI = 2 individuals.

REMARKS: The recovery of ptarmigan elements at both Bath Co. cave sites was especially significant in light of the birds' present distribution and habitat requirements. Northern Quebec and Newfoundland represent the most southern reaches of the bird's range in eastern North America, approximately 1,800 km north-northeast of Bath Co. Ptarmigan are birds of the open tundra, and their occurrence as far south as west-central Virginia is indicative of the former presence of open or semi-open expanses of tundra that must have covered the northern Appalachian Mountains during full-glacial to late Pleistocene times. The recovery of caribou (*Rangifer tarandus* L.) elements from Sullivan Co. caves in eastern Tennessee (Guilday, Hamilton, and Parmelee, 1975) also serves to substantiate the former southern extension of a tundra-like habitat and related climatic conditions to at least the central Appalachians. In a summary of their findings based on pollen data, Maxwell and Davis (1972:506) state

that "When the Wisconsin ice sheet stood at its maximum position, tundra vegetation bordered the ice sheet. In the eastern United States, tundra extended at least 300 kilometers due south of the ice border at 2,700 feet (800 meters) elevation on the Allegheny Plateau. Spruce and jack (and/or red) pine forest grew at lower elevations in Virginia."

Anatomical differences among the species of *Lagopus* also are extremely subtle, and many of the fragmentary or abraded elements are difficult to distinguish from those of *Bonasa* or *Canachites*. The large, open circular pneumatic foramen of the humerus appears to be one of the more valid characters separating ptarmigan from the other two genera of grouse. The humerus and tarsometatarsus from Clark's Cave (Fig. 13) were verified as *L. mutus* by Alexander Wetmore (pers. comm. 1/29/73). The latter element is especially difficult to identify to species, however, and it is possible that the willow ptarmigan, *L. lagopus* (Linnaeus), is represented. Both species occupy a similar range in northeastern Canada, but the willow ptarmigan prefers areas of

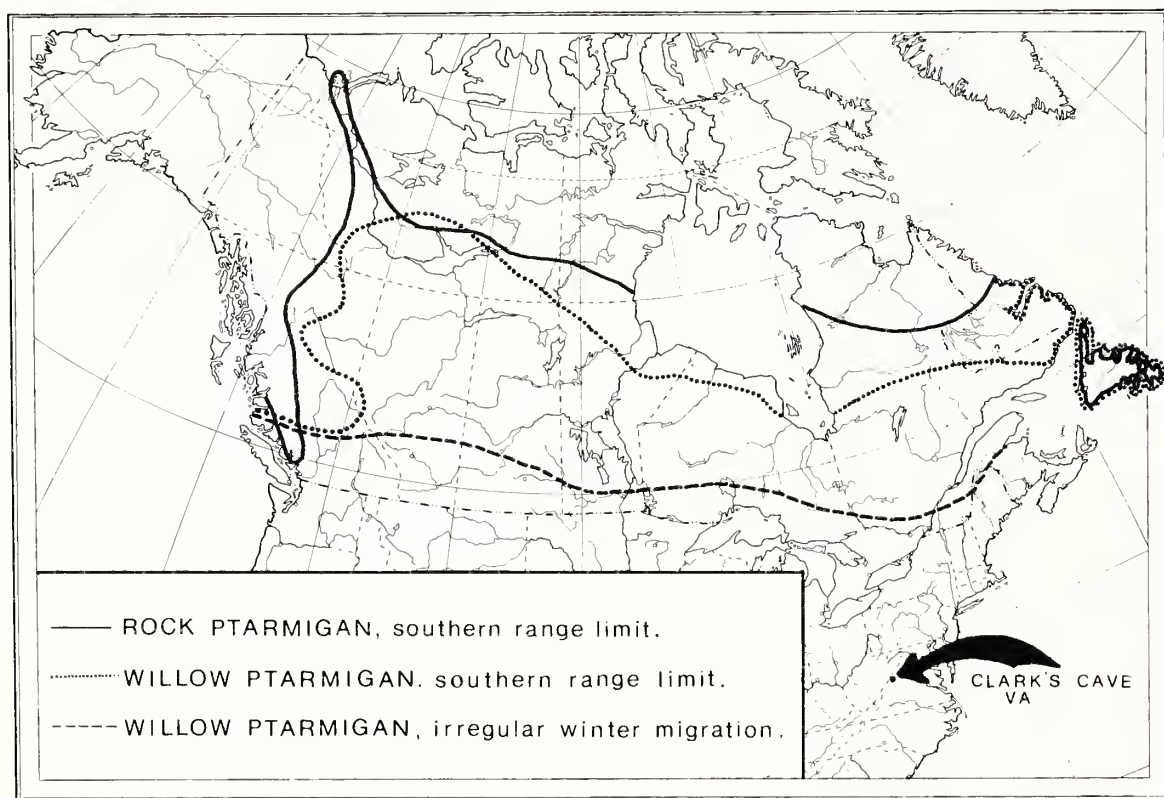


Fig. 12. Modern ranges of rock ptarmigan, *Lagopus mutus* (Montin), and willow ptarmigan, *Lagopus lagopus* (Linnaeus), adapted from Godfrey, 1966. Ptarmigan fossils present in Clark's Cave local fauna.



Fig. 13. *Lagopus cf. mutus* (Montin), Clark's Cave local fauna, Bath County, Virginia, CM 29627. Upper: left tarsometatarsus; lower: left humerus.

stunted and scattered trees—a habitat perhaps characteristic of the Allegheny and Shenandoah mountains in the late glacial times. Occasional winter wanderers have been recorded as far south as Maine (Kenduskeag) and northern New York (Lewis County), 680 km north of Clark's Cave (5th A.O.U. "Check-list," p.131).

However, because of certain subtle but possibly significant osteological differences noted by Storrs Olson (letter Olson/Parmalee, 10/24/75) between the cave elements and those of the rock and willow ptarmigan skeletons in the collections of the USNM, specific determinations should be considered tentative until these differences can be resolved.

cf. Pedicetes phasianellus (Linnaeus)—Sharp-tailed Grouse

MATERIAL: CM 29628. 2 right and 2 left carpometacarpals;

sections of 3 coracoids, 1 ulna, 1 tarsometatarsus, 1 tibiotarsus, 1 humerus, 1 femur. MNI = 3 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29705. 1 nearly complete right and 1 left carpometacarpus, 4 distal ends of tibiotarsi. MNI = 4 individuals.

REMARKS: Remains of at least four sharp-tailed grouse were identified from Natural Chimneys, Va. The former presence of this grouse in west-central Virginia is also of special interest, since today its closest range proximity to the Bath County sites is northern Wisconsin and Michigan and southern Ontario (Fig. 14). Osteologically, it and the prairie chicken, *Tympanuchus cupido* (Linnaeus), are extremely similar. The synsacrum is considered by some avian osteologists to be the only specifically diagnostic element (e.g. Wetmore, 1959), so the Clark's Cave and Back Creek Cave No. 2 material lends itself only to tentative determination. Presence of this species, based upon the synsacrum, was definitely

established at New Paris No. 4, Pa. during the late Pleistocene.

The overall greater length or more robust limb elements tend to differentiate bones of either *Pedioecetes* or *Tympanuchus* from those of *Bonasa* and *Canachites*. Nevertheless, another 4 tarsometatarsi and 2 carpometacarpals (CM 29629) from Clark's Cave compare closely with those of sharp-tailed grouse (*Pedioecetes* tarsometatarsi are proportionately shorter and less robust than *Tympanuchus*), yet could conceivably be from large male ruffed grouse. The sharp-tailed grouse is unknown from the state in historic times, and the prairie chicken (heath hen, *T. c. cupido*) "possibly" occurred in eastern Virginia along the Atlantic seaboard (5th A.O.U. "Check-list":136). However, the sharp-tailed grouse is certainly the "boreal" species of the two, and considering its habitation of forested regions and especially areas of low thickets and open glades or savannas, it would have been well adapted to the late Pleistocene habitat of the Appalachians.

Family:Phasianidae—Quails and Pheasants

Colinus virginianus (Linnaeus)—Bobwhite

MATERIAL: CM 29630. Complete (or sections of) items including 3 tarsometatarsi, 3 coracoids, 2 humeri, 2 carpometacarpals, sternum, radius. MNI = 2 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29706. Radius, ulna; 2 incomplete carpometacarpals, 1 tarsometatarsus, phalanx I. MNI = 2 individuals.

REMARKS: A common bird in the open and semi-open brushy areas throughout the state, but rare in heavily forested regions.

Family: Meleagrididae—Turkeys

Meleagris gallopavo Linnaeus—Turkey

MATERIAL: CM 29632. Phalanx I; sections of scapula, humerus, tarsometatarsus, radius. MNI = 1 individual.

REMARKS: Except for the complete phalanx I, the turkey elements are fragmented and, in the case of the humerus shaft, rodent gnawed. It was reported originally to have been abundant throughout the state (Murray 1952:44). However, even the largest of raptors would have difficulty in capturing adult turkeys, and therefore the paucity of turkey remains at owl roost sites like Clark's Cave is not unexpected.

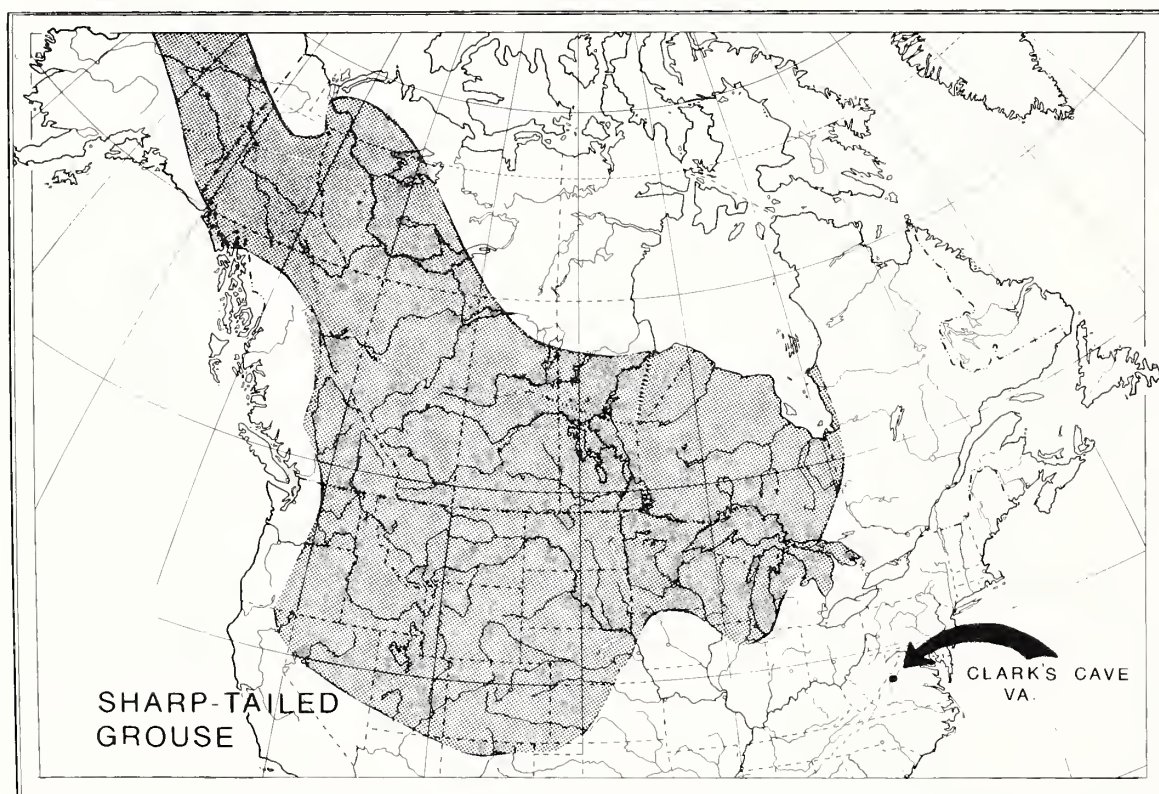


Fig. 14. Modern range of sharp-tailed grouse, *Pedioecetes phasianellus* (Linnaeus), adapted from Godfrey, 1966. Present in Clark's Cave local fauna.

Order: Gruiformes

Family: Rallidae—Rails, Gallinules, and Coots

cf. *Rallus limicola* Vieillot—Virginia Rail

MATERIAL: CM 29633. Distal third of right tibiotarsus. MNI = 1 individual.

Porzana carolina (Linnaeus)—Sora Rail

MATERIAL: CM 29634. Incomplete sections of 2 tarsometatarsi, 1 tibiotarsus, 1 coracoid, 2 humeri, 2 carpometacarpals. MNI = 2 individuals.

REMARKS: Apparently a fairly common migrant and nesting bird locally in western Virginia (Blacksburg), the Virginia rail would not be unexpected in the marshy grasslands bordering the Cowpasture River. The sora, although less numerous in the western part of the state than it is along the coastal tidewater marshes, is reportedly not uncommon locally in inland marshes and river flood plains. A fragmented right carpometacarpus (CM 29635) of what appears to be an additional species of small rail (yellow or black?) was recovered at Clark's Cave.

cf. *Gallinula chloropus* (Linnaeus)—Common Gallinule

MATERIAL: CM 29636. Distal end of lower mandible. MNI = 1 individual.

REMARKS: This section of bill is too fragmentary to permit an unquestionable determination but, on the basis of comparative specimens examined, it appears to be this species rather than eoot (*Fulica americana*) or purple gallinule (*Porphyryla martinica*). There are numerous migration and nesting records of the common gallinule in Virginia (Murray, 1952:46,47). Wet lowlands bordering the Cowpasture River could have afforded this gallinule, as well as other marsh-dwelling species like the rails and woodcock, suitable nesting habitat.

Order: Charadriiformes

Family: Charadriidae—Plovers and Turnstones

Pluvialis dominica (Muller)—
American Golden Plover

MATERIAL: CM 29637. Complete left tarsometatarsus. MNI = 1 individual.

REMARKS: Murray (1952:48) states that the American golden plover is rare inland, but he lists fall occurrence of this bird at Roanoke and Blacksburg.

Family: Scolopacidae—

Woodcock, Snipe, and Sandpipers

Philohela minor (Gmelin)—American Woodcock

MATERIAL: CM 29638. Complete (or sections of) items in-

cluding 6 tarsometatarsi, 2 femora, 2 scapulae, 3 coracoids, 2 carpometacarpals, 2 humeri, 2 quadrates, radius, ulna. MNI = 4 individuals.

REMARKS: The American woodcock is reported to be a rare to uncommon summer resident throughout most of Virginia, but Murray (1952:49) does list young observed in Shenandoah Park, Bath, and Alleghany counties. Marshes 1.6 km south and 3 km northeast of Clark's Cave could have provided suitable habitat.

Capella gallinago (Linnaeus)—Common Snipe

MATERIAL: CM 29639. Complete left coracoid. MNI = 1 individual.

cf. *Actitis macularia* (Linnaeus)—Spotted Sandpiper

MATERIAL: CM 29640. 2 tarsometatarsi, 2 femora, 1 carpometacarpal, 3 coracoids; incomplete sections of 2 humeri, 1 tibiotarsus. MNI = 2 individuals.

? *Tringa solitaria* Wilson—Solitary Sandpiper

MATERIAL: CM 29641. 2 right distal end sections of tarsometatarsi. MNI = 2 individuals.

Indeterminate spp.—sandpipers/plovers

MATERIAL: CM 29642. Sections of sternum, 2 humeri, 2 ulnas, radius, 3 tibiotarsi, 3 tarsometatarsals, carpometacarpus, 10 coracoids. MNI = 6 or 7 individuals.

REMARKS: Elements of the numerous small species of plovers and sandpipers are often difficult to identify, especially when incomplete or abraded. Several complete, or nearly complete small sandpiper bones from Clark's Cave compared most favorably with those of the spotted and least sandpipers. Five of the indeterminate coracoids fall within the size range of the spotted/solitary/least group. In Virginia the spotted sandpiper is a common local summer resident. One was observed by C. O. Handley, Jr. (pers. comm. 10/7/74) on the bank of the Cowpasture River at Clark's Cave on August 13, 1974. All three species occur in varying numbers as transients or migrants within the state.

cf. *Limosa* Brisson—Godwit

MATERIAL: CM 29643. Sections of 3 right distal tibiotarsals, right coracoid, proximal left humerus. MNI = 3 individuals.

REMARKS: In addition to these five fragmentary elements, three other large "shorebird" bone pieces (coracoid, 2 ulnae) from Clark's Cave fall within the godwit-willet size range. These remains, because of their fragmented or eroded condition, could not be specifically identified with certainty. Although both the marbled godwit, *Limosa fedoa* (Linnaeus), now on the increase, and the Hudsonian godwit, *L. hae-*

mastica (Linnaeus), were formerly common along the coast during migration, there are apparently no inland records. The willet, *Catoptrophorus semipalmatus* (Gmelin), a species similar osteologically and in size to the godwits, was reported from Natural Chimneys, Va. by Wetmore. However, after careful comparison with *Limosa* and *Catoptrophorus*, the Clark's Cave material, especially the tibiotarsi, appears to be one of the godwits.

Order: Columbiformes

Family: Columbidae—Pigeons and Doves

Ectopistes migratorius (Linnaeus)—Passenger Pigeon

MATERIAL: CM 29644. A total of approximately 275 elements, complete and incomplete; wing and leg bones predominate. MNI = 30 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29707. One bill and 24 wing and leg elements. MNI = 8 individuals.

REMARKS: Considering the former abundance of the passenger pigeon in eastern North America, it is not surprising to find quantities of their remains in early hawk or owl roost deposits like Clark's Cave and Back Creek Cave No. 2. Murray (1952:61) refers to several accounts relating the pigeons' former abundance in Virginia, including Bath County, and mentions a roost (in 1872) in Buckingham County that reportedly covered an area of four square miles. Remains of *E. migratorius* at Clark's Cave accounted for nearly 28% of the total number of identified bird bones (excluding indeterminate passerines). Until the last two decades of the 19th century, this pigeon appears to have been one of the major food items of raptors occupying these cave sites.

Order: Cuculiformes

Family: Cuculidae—Cuckoos and Roadrunners

Coccyzus Vieillot—Cuckoo

MATERIAL: CM 29645. Incomplete right carpometacarpus. MNI = 1 individual.

REMARKS: The yellow-billed cuckoo, *Coccyzus americanus* (Linnaeus), is reported to be considerably more common in Virginia than the black-billed cuckoo, *C. erythrophthalmus* (Wilson), although both species could be expected in the vicinity of Clark's Cave. Even if the carpometacarpus had been complete, it is doubtful that it could have been identified to species.

Order: Strigiformes

Family: Strigidae—Typical Owls

cf. *Otus asio* (Linnaeus)—Screech Owl

MATERIAL: CM 29646. Section of a premaxilla and nasal

process. MNI = 1 individual.

Bubo virginianus (Gmelin)—Great Horned Owl

MATERIAL: CM 29647. Incomplete section of left articular; sclerotic bone, possibly referable to this species. MNI = 1 individual.

Asio otus (Linnaeus)—Long-eared Owl, *Asio flammeus* (Pontoppidan)—Short-eared Owl, or both

MATERIAL: CM 29648. Sections of 3 tarsometatarsi, humerus, coracoid, 2 femora, 4 ulnae. MNI = 3 individuals.

Aegolius acadicus (Gmelin)—Saw-whet Owl

MATERIAL: CM 29649. Complete tarsometatarsus; sections of radius, ulna, femur, coracoid. MNI = 1 individual.

Owl sp.

MATERIAL: CM 29650. Claw, 15 metapodials.

MATERIAL (Back Creek Cave No. 2): CM 29708. Section of sternum (screech owl? : CM 29708), distal end of tibiotarsus (*Aegolius* sp.? : CM 29720), claw (CM 29721), and premaxilla fragment, possibly *A. acadicus* (CM 29719).

REMARKS: Both the screech owl and the great horned owl are fairly common locally throughout the state. Murray (1952:63-64) reports the long-eared owl as a rare resident, the short-eared owl as rather common in the coastal areas, also infrequent in suitable habitat throughout the mountains as a migrant and winter visitor, and the saw-whet owl as being a rare winter visitor in Virginia (C. O. Handley, Jr. saw one near Clark's Cave, Panther Gap, Sept. 7, 1975). Except for metapodials, the complete tarsometatarsus of a saw-whet owl, and the nearly complete tarsometatarsus of *Asio*, all other elements of these birds were fragmentary or eroded. The latter bone is probably referable to *Asio otus*, a species of owl associated with dense stands or thickets of coniferous trees. Clark's Cave is presently (1974) being used as a feeding/roost site by barn owls, but no remains of this bird were encountered in the deposit.

Although the long-eared owl is capable of taking prey the size of ruffed grouse and cottontails, most of its food consists of small rodents and, to a lesser extent, small birds. Screech owls utilize both small birds and rodents, while the saw-whet owl feeds primarily on small rodents. The great horned owl is known to take mammals like skunks and porcupine, and birds as large as the Canada goose, turkey, and the red-tailed hawk have been recorded as prey of this owl. Data on the food habits of the great horned owl provided by Bent (1938:306-312) are indicative of the variety of prey species

remains that might be expected at a roost site. It is apparent from the variation in size of the animals represented in the Clark's Cave deposit that both large and small raptorial birds contributed.

Order: Caprimulgiformes

Family: Caprimulgidae—Goatsuckers

Chordeiles minor (Forster)—Common Nighthawk

MATERIAL: CM 29651. Incomplete right humerus and right coracoid. MNI = 1 individual.

REMARKS: A common summer resident and migrant over much of the state.

Order: Apodiformes

Family: Apodidae—Swifts

Chaetura pelagica (Linnaeus)—Chimney Swift

MATERIAL: CM 29652. Complete left carpometacarpus. MNI = 1 individual.

REMARKS: A common summer resident throughout the state.

Order: Coraciiformes

Family: Alcedinidae—Kingfisher

Megasceryle alcyon (Linnaeus)—Belted Kingfisher

MATERIAL: CM 29653. Incomplete right humerus, left carpometacarpus, and left coracoid. MNI = 1 individual.

REMARKS: The belted kingfisher occurs as a permanent resident in Virginia, varying in abundance locally depending upon season and general habitat. Birds were observed by C. O. Handley, Jr. (letter Handley/Parmalee, 10/7/74) along the Cowpasture River in September, 1974. Wetmore reported it from Natural Chimneys, Va.

Order: Piciformes

Family: Picidae—Woodpeckers

Colaptes auratus (Linnaeus)—Common Flicker

MATERIAL: CM 29654. 1 complete left carpometacarpus, incomplete elements including 1 ulna, 4 carpometacarpals, 3 tarsometatarsi, femur, coracoid. MNI = 3 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29709. 3 incomplete carpometacarpals, femur, tarsometatarsus and 2 humeri (juvenile ?; also a tibiotarsus and tarsometatarsus section of a juvenile woodpecker, possibly flicker). MNI = 2 individuals.

Dryocopus pileatus (Linnaeus)—

Pileated Woodpecker

MATERIAL: CM 29655. 2 incomplete right humeri, right scapula. MNI = 2 individuals.

cf. *Centurus carolinus* (Linnaeus)—

Red-bellied Woodpecker

MATERIAL: CM 29656. 1 partial right and 1 partial left humerus. MNI = 1 individual.

? *Melanerpes erythrocephalus* (Linnaeus)—

Red-headed Woodpecker

MATERIAL (Back Creek Cave No. 2): CM 29710. Distal end of left humerus. MNI = 1 individual.

Sphyrapicus varius (Linnaeus)—

Yellow-bellied Sapsucker

MATERIAL: CM 29657. Proximal end of left humerus. MNI = 1 individual.

Dendrocopos villosus (Linnaeus)—

Hairy Woodpecker

MATERIAL: CM 29658. Proximal end of right humerus, nearly complete right tibiotarsus. MNI = 1 individual.

MATERIAL (Back Creek Cave No. 2): CM 29711. Complete left carpometacarpus and tarsometatarsus, distal end of right tarsometatarsus. MNI = 1 individual.

Dendrocopos pubescens (Linnaeus)—

Downy Woodpecker

MATERIAL: CM 29659. 1 incomplete left carpometacarpus, distal end of left tarsometatarsus. MNI = 1 individual.

Woodpecker ssp.

MATERIAL: CM 29660. Sections of femur, radius, carpometacarpus, and 2 tarsometatarsi. MNI = probably 2 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29712. Sections of 4 tarsometatarsi (1 juvenile), tibiotarsus, carpometacarpus and ulna. MNI = 3 individuals.

REMARKS: All species of woodpeckers represented in these two cave deposits are considered permanent residents in Virginia, and all may be found today in Bath County. The indeterminate woodpecker elements all appear to be within the size range of the red-bellied/red-headed/hairy woodpecker group.

Woodpeckers appear to be particularly susceptible to predation by raptorial birds, and their remains often occur in cave and rock-shelter deposits. To illustrate, approximately 400 bird bones were recovered at the Raven Rocks Site, Belmont County, Ohio (Shane and Parmalee, in press). At least 15 species were represented and nearly 12% of the bones were those of woodpeckers. Of these, at least one-third were nestlings or juveniles.

Order: Passeriformes

Family: Tyrannidae—Flycatchers

Empidonax cabanis—Flycatcher

MATERIAL: CM 29661. Complete right humerus. MNI = 1 individual.

REMARKS: This element compares closely with the yellow-bellied flycatcher, *E. flaviventris* (Baird and

Baird), and the Acadian flycatcher, *E. virescens* (Vieillot). The former species is an uncommon migrant in Virginia, the latter a common summer resident. C. O. Handley, Jr. heard several Acadian flycatchers singing along the Cowpasture River at Clark's Cave in June and August, 1974 (letter Handley/ Parmalee, 10/7/74).

Family: Alaudidae—Larks

cf. *Eremophila alpestris* (Linnaeus)—Horned Lark

MATERIAL: CM 29662. Complete left coracoid. MNI = 1 individual.

REMARKS: Although this coracoid compares well with the horned lark, a bird of the open grasslands, identification must remain tentative. The coracoid has proved to be specifically non-diagnostic in a large number of passerine birds, especially in those groups containing numerous closely related species.

Family: Hirundinidae—Swallows

Petrochelidon pyrrhonota (Vieillot)—Cliff Swallow

MATERIAL: CM 29663. Complete (or sections of) items including 13 humeri, 4 ulnae, carpometacarpus, coracoid, and tarsometatarsus. In addition, there are 12 fragmented or abraded swallow elements (CM 29664) that are probably referable to this species. MNI = 9 individuals.

REMARKS: The cliff swallow, a local summer resident in Virginia, may still be found nesting in natural cliff sites, although nests of colonies are most often observed in barn eaves and under bridge floors and railings. Apparently one or more of the hawks or owls utilizing Clark's Cave preyed upon local nesting colonies of these swallows. It is of interest to note, however, that Bent (1942:480) states that "Predaceous birds cannot be considered as serious enemies of the cliff swallow." At least eight cliff swallows were represented in the avifauna of Natural Chimneys, Va. C. O. Handley, Jr. saw them flying near Clark's Cave in 1974.

Family: Corvidae—Jays, Magpies, and Crows

Perisoreus canadensis (Linnaeus)—Gray Jay

MATERIAL: CM 29665. Complete left ulna, proximal end of left humerus. MNI = 1 individual.

REMARKS: Although the ulna recorded here as *P. canadensis* may be subject to question because this element in general lacks good diagnostic characters, both it and the section of humerus (a good diagnostic bone) compare favorably with gray jay. The former occurrence of this bird as far south as the Shenandoah Mountains area was established when remains of it were encountered in the Natural Chim-

neys, Va., deposit. The gray jay is associated with boreal coniferous forests, and its former presence in Bath and Augusta counties (as an established resident and not as a casual visitor) is suggestive of a once-cooler climate and a possibly different spruce-fir forest association.

Cyanocitta cristata (Linnaeus)—Blue Jay

MATERIAL: CM 29666. Incomplete left carpometacarpus. MNI = 1 individual.

MATERIAL (Back Creek Cave No. 2): CM 29713. Proximal half of right humerus, incomplete right carpometacarpus and femur. MNI = 1 individual.

Corvus brachyrhynchos Brehm—Common Crow

MATERIAL: CM 29667. Fragmentary distal end of left humerus, proximal end of right tibiotarsus, right scapula. MNI = 1 individual.

REMARKS: Both the blue jay and common crow occur throughout Virginia as permanent residents and may be seen occasionally today in the vicinity of Clark's Cave.

Family: Paridae—Titmice

Parus Linnaeus—Chickadee

MATERIAL: CM 29668. Proximal half of right humerus, fragment of proximal end of left humerus. MNI = 1 individual.

Parus bicolor Linnaeus—Tufted Titmouse

MATERIAL: CM 29669. Proximal end of left humerus. MNI = 1 individual.

REMARKS: Both the Carolina chickadee, *Parus carolinensis* Audubon, and the black-capped chickadee, *Parus atricapillus* Linnaeus, can be expected in the vicinity of Clark's Cave. Chickadees and the tufted titmouse are fairly-common to common statewide.

Family: Sittidae—Nuthatches

cf. *Sitta canadensis* Linnaeus—
Red-breasted Nuthatch

MATERIAL: CM 29670. Complete right humerus. MNI = 1 individual.

REMARKS: This nuthatch and the white-breasted nuthatch, *Sitta carolinensis* Latham, both occur in western Virginia, varying in abundance locally from rare to common.

Family: Certhiidae—Creepers

Certhia familiaris Linnaeus—Brown Creeper

MATERIAL: CM 29671. 2 complete left tarsometatarsi. MNI = 2 individuals.

REMARKS: Murray (1952:76) records the brown

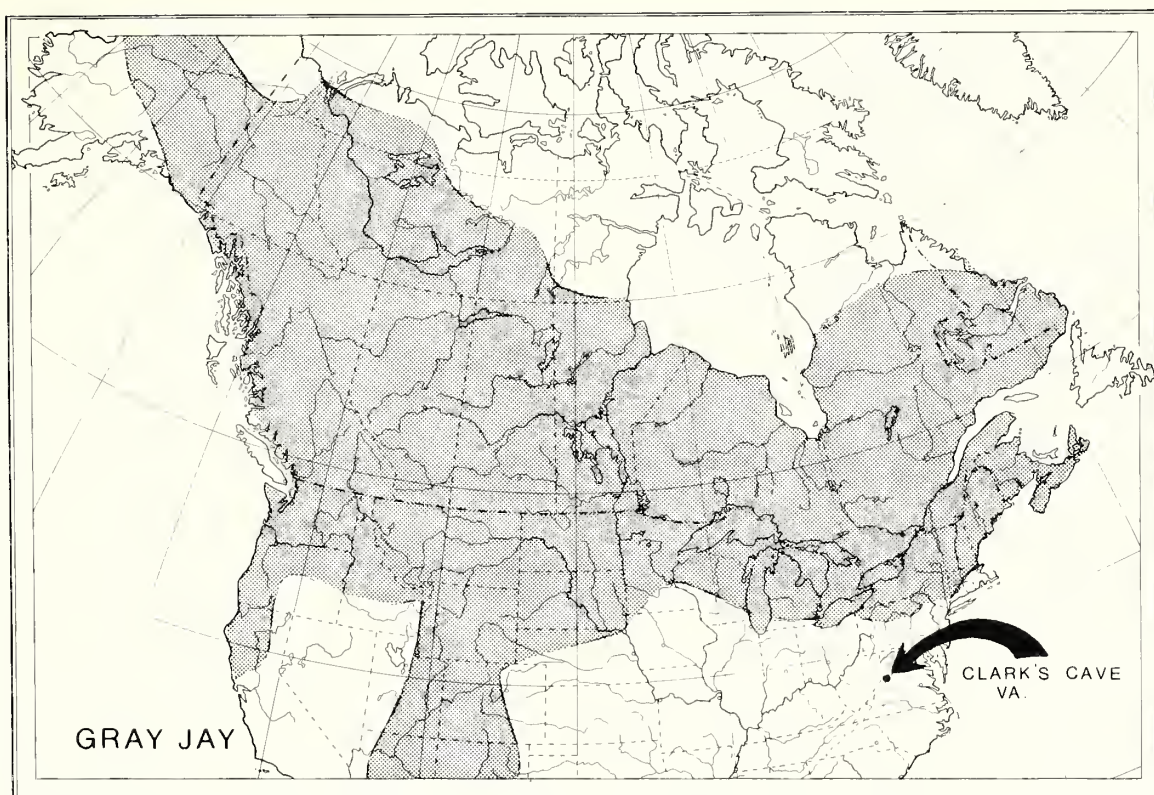


Fig. 15. Modern range of gray jay, *Perisoreus canadensis* (Linnaeus), adapted from Godfrey, 1966. Present in Clark's Cave local fauna.

creeper as a generally common winter resident and migrant in Virginia. It is also a local summer resident in the mountains. C. O. Handley, Jr. observed several nests at Mountain Lake, Giles County.

Family: Troglodytidae—Wrens

? *Cistothorus platensis* (Latham)—

Short-billed Marsh Wren

MATERIAL: CM 29672. Right humerus, lacking a portion of the proximal end. MNI = 1 individual.

REMARKS: Although this humerus section compares favorably with *C. platensis*, identification can only be tentative because of its incompleteness. During spring and fall migrations this bird is a rare transient, as is the longbilled marsh wren, *Telmadodytes palustris* (Wilson), in the western and other inland regions of the state.

Family: Mimidae—Mockingbirds and Thrashers

cf. *Toxostoma rufum* (Linnaeus)—Brown Thrasher

MATERIAL: CM 29673. Proximal half of left humerus; incomplete right coracoid, possibly referable to *T. rufum*. MNI = 1 individual.

REMARKS: A common to abundant bird throughout the state.

Family: Turdidae—

Thrushes, Solitaires, and Bluebirds

Turdus migratorius Linnaeus—Robin

MATERIAL: CM 29674. Complete right and left carpometacarpus, right ulna, radius and tarsometatarsus; incomplete sternum, proximal left humerus, right carpometacarpus. In addition, a complete left femur and the distal halves of a right tibiotarsus, tarsometatarsus, and humerus are also probably robin. MNI = 2 individuals.

Hylocichla Baird—Thrush

MATERIAL: CM 29675. Nearly complete right and left humeri. MNI = 2 individuals.

cf. *Sialia sialis* (Linnaeus)—Eastern Bluebird

MATERIAL: CM 29676. Incomplete proximal half of left humerus. MNI = 1 individual.

REMARKS: The robin is an abundant summer resident and migrant, and locally common winter resident in the state. The two humeri determined as *Hylocichla* fall within the size range of the veery/

hermit/gray-cheeked/Swainson's thrush group, all of which may be found in the vicinity of Clark's Cave at one season or the other. The eastern bluebird is a permanent resident in Virginia, primarily inhabiting the semi-open brush and grassland areas.

Family: Montacillidae—Wagtails and Pipits

? *Anthus spinoletta* (Linnaeus)—Water Pipit

MATERIAL: CM 29717. Incomplete right coracoid. MNI = 1 individual.

REMARKS: The distal or head portion of this element compares favorably with the water pipit. The overall head shape and extremely deep groove between the glenoid facet and the bicipital attachment (external view) appear diagnostic. However, determination is tentative because of the fragmentary condition of the coracoid. Water pipits are considered to be irregular migrants and winter visitors in most of Virginia (Murray, 1952:84).

Family: Bombycillidae—Waxwings

Bombycilla cedrorum Vieillot—Cedar Waxwing

MATERIAL: CM 29677. Complete right humerus. MNI = 1 individual.

REMARKS: A permanent resident, but erratic in occurrence in western Virginia.

Family: Parulidae—Wood Warblers

cf. *Dendroica coronata* (Linnaeus)—
Yellow-rumped Warbler

MATERIAL: CM 29679. Nearly complete right humerus. MNI = 1 individual.

? *Seiurus Swainson*—Waterthrush

MATERIAL: CM 29680. Nearly complete right humerus. MNI = 1 individual.

Warbler ssp.

MATERIAL: CM 29680. Complete (or sections of) items including 2 humeri, 2 carpometacarpals, 2 tibiotarsi, 2 ulnae, coracoid. MNI = 2 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29722. Nearly complete left humerus possibly referable to golden-winged warbler, *Vermivora chrysoptera* (Linnaeus). MNI = 1 individual.

REMARKS: Murray (1952:92) records the myrtle warbler (yellow-rumped warbler) as an "abundant transient everywhere; uncommon to abundant winter visitor as far west as Lexington; occasional in winter at Blacksburg." In addition to these few elements identified as warbler, many of the fragmentary or abraded bones recorded as Indeterminate Passerines are probably from species within this Family.

Family: Icteridae—

Meadowlarks, Blackbirds, and Orioles

cf. *Dolichonyx oryzivorus* (Linnaeus)—Bobolink

MATERIAL: CM 29681. Proximal end of right humerus. MNI = 1 individual.

cf. *Sturnella Vieillot*—Meadowlark

MATERIAL: CM 29682. Distal end of left humerus. MNI = 1 individual.

Agelaius phoeniceus (Linnaeus)—

Redwinged Blackbird

MATERIAL: CM 29683. Complete left humerus, right ulna and carpometacarpus. MNI = 1 individual.

cf. *Icterus spurius* (Linnaeus)—Orchard Oriole

MATERIAL: CM 29684. Complete right humerus. MNI = 1 individual.

REMARKS: The four icterids identified from Clark's Cave occur as permanent residents, migrants, or nesting birds in the western part of the state. Identifications based on incomplete elements or those lacking good diagnostic characters (e.g., the ulna) are recorded as tentative. However, after comparison of elements with these species and those of closely related blackbirds (e.g., Baltimore oriole and orchard oriole), it is felt that the determinations are valid.

Family: Thraupidae—Tanagers

Piranga Vieillot—Tanager

MATERIAL: CM 29685. Premaxilla. MNI = 1 individual.

REMARKS: The scarlet tanager, *Piranga olivacea* (Gmelin), is widespread and an abundant summer resident. The summer tanager, *Piranga rubra* (Linnaeus), is an uncommon and local resident in western Virginia. On the basis of this incomplete mandible section from Clark's Cave, it was not possible to identify the species.

Family: Fringillidae—

Grosbeaks, Finches, Sparrows, and Buntings

cf. *Pinicola enucleator* (Linnaeus)—Pine Grosbeak

MATERIAL: CM 29686. Anterior section of lower mandible. MNI = 1 individual.

MATERIAL (Back Creek Cave No. 2): CM 29714. Anterior section of lower mandible. MNI = 1 individual.

REMARKS: Although similar in size and general structure to the mandibles of cardinal, rose-breasted grosbeak, and evening grosbeak, these two cave specimens compare most closely with *P. enucleator*, based on the wider, more U-shaped inner angle of the symphysis and the distance of the splenial de-

pression from the tip. Murray (1952:105) records one specimen collected in Shenandoah Park and one observed at Richmond. If the determination of these bill sections is correct, the former occurrence of this grosbeak in western Virginia represents local winter stragglers or perhaps reflects the cooler climate and spruce forests of the late Pleistocene—a habitat type now occupied by this bird.

Loxia Linnaeus—Crossbill

MATERIAL: CM 29718. Section of premaxilla. MNI = 1 individual.

MATERIAL (Back Creek Cave No. 2): CM 29723. Complete right humerus; distal end of a right humerus, probably referable to *Loxia*. MNI = 2 individuals.

REMARKS: The red crossbill, *Loxia curvirostra* Linnaeus, is considered an erratic visitor at all seasons in the Virginia mountains, and the white-winged crossbill, *Loxia leucoptera* Gmelin, an infrequent winter visitor (Murray, 1952:106).

Indeterminate sparrow ssp.

MATERIAL: CM 29687. 2 incomplete carpometacarpals, 2 humeri, coracoid.

REMARKS: An additional right humerus, tentatively determined as vesper sparrow, *Pooecetes gramineus* (Gmelin), was the only complete diagnostic element recovered of this group of fringillids, which are especially difficult to identify osteologically. The vesper sparrow is listed as a summer resident from Richmond west (Murray, 1952:109).

Junco cf. *hyemalis* (Linnaeus)—Dark-eyed Junco

MATERIAL: CM 29688. 3 complete humeri, premaxilla. MNI = 2 individuals.

MATERIAL (Back Creek Cave No. 2): CM 29715. Complete left humerus. MNI = 1 individual.

REMARKS: Juncos are common winter residents throughout the state, and permanent residents in the mountains above 758 m.

MAMMALIA—Mammals

Order: Insectivora—Insectivores

Family: Soricidae—Shrews

Genus *Sorex* Linnaeus—Long-tailed shrews

Sorex arcticus Kerr—Arctic shrew

MATERIAL: CM 24540: 1 partial skull. CM 24581: 13 left, 12 right mandibles. MNI = 13 individuals.

Sorex cinereus Kerr—Masked shrew

MATERIAL: CM 24580. 67 left, 61 right mandibles. MNI = 67 individuals.

Sorex dispar Batchelder—Big-tailed or rock shrew

MATERIAL: CM 24583. 2 left, 4 right mandibles. MNI = 4 individuals.

Sorex fumeus Miller—Smoky shrew

MATERIAL: CM 24582. 9 left, 10 right mandibles. MNI = 10 individuals.

Sorex palustris Richardson—Water shrew

MATERIAL: CM 24587. 3 left, 7 right mandibles. MNI = 7 individuals.

Sorex, ?species

MATERIAL: CM 24584: 17 left, 12 right fragmentary large mandibles (*S. fumeus*/*S. arcticus*/*S. palustris*); 9 left, 10 right fragmentary small mandibles (*S. cinereus*/*S. dispar*). CM 24585: unidentified skull fragments. MNI = 26 individuals.

REMARKS: All five species of *Sorex* from the deposit inhabit at least some portion of the Appalachian Mountain chain. *Sorex arcticus*, the second commonest soricid from the Clark's Cave deposit, occurs only as far south as New Brunswick, 1,440 km northeast of Clark's Cave. It ranges across the continent, from eastern Quebec to Alaska, in boreal habitats ranging from coniferous forest to tundra. Banfield, 1974, suggests that it is typical of subclimax or transitional vegetation stages, and that while it is frequently taken in bogs and marshes, it favors a habitat slightly drier than that of other species of shrews. The water shrew, *S. palustris*, still occurs in the Appalachian Mountains south, at increasingly greater elevations, into the Great Smokies, approximately 240 km southwest of Clark's Cave (Linzey & Linzey, 1971). It has been taken in Randolph County, W. Va., and in all probability does occur in suitable mountain streamside habitats above 760 m in western Virginia (Handley & Patton, 1947). It is no longer present in the Clark's Cave area, but has recently been trapped within 15 km of the cave at a higher altitude (Pagels and Tate, 1975). Despite the riverside location of the site, *S. palustris* remains were not common (Table 6). Only *S. dispar* remains were fewer in number, reflecting the specialized habitats of these two shrews.

The peculiar habitat of the big-tailed shrew, *S. dispar*, confined to and generally deep into rocky talus, contributes to its apparent rarity. Handley (1956b) trapped it near the crest of Big Mountain at 1,200 m elevation, Giles County, Va., southwest of Clark's Cave. It has subsequently been found to be fairly common in four areas near Mountain Lake, Giles County, and also has been taken on Whitetop

and Clinch Mountains. It may be expected in cool, moist, boulder and talus fields, above 600 m in the mountains (Handley & Patton, 1947). It occurs in the Clark's Cave talus today and was trapped there in 1974 by C. O. Handley, Jr. and associates. *S. dispar* occurs throughout the Appalachian chain, from Maine to Tennessee and North Carolina (Hall & Kelson, 1959). A smaller species, *S. gaspensis*, occurs in the Gaspé Peninsula of eastern Quebec, 240 km north of the range of *S. dispar*. If *S. gaspensis* is a subspecies of *S. dispar*, as some have suggested (Jackson, 1928; Banfield, 1974) this suggests that, in the northern limits of its range, *S. dispar* is not as closely confined to a talus habitat, but finds the microhabitat it requires in surface forest litter rather than in the labyrinthine cold air sinks of rock talus refuges of the South. Goodwin states (Jackson, 1928:91) that the habits of *S. gaspensis* appear to be similar to those of *S. palustris*. Although not directly compared with *S. gaspensis*, the Clark's Cave specimens agree in size with those of *S. dispar* (Table 7). *S. dispar* may therefore have been more broadly distributed during past boreal phases. This is suggested by its presence at New Paris No. 4, Pa. (4 individuals), in a region of well-drained rolling hills not physiographically suited for *S. dispar* today. The modern range of *S. dispar* suggests that, at least during Wisconsinan times, it was confined to the Appalachian region and was unable to cross or circumvent the St. Lawrence/Great Lakes water barrier into east-central Canada following glacial retreat.

The masked shrew, *S. cinereus*, the most widely distributed North American insectivore today, found in most of northern North America from Alaska to Labrador south, and in the mountains to New Mexico and North Carolina, was by far the commonest long-tailed shrew recovered from the deposit. It is possible that some of the remains may be those of the southern Bachman's shrew, *S. longirostris*. Identification was based solely on lower jaws, because of the fragmentary condition of the remains. Except for a smaller average size, lower jaws of these two species cannot be differentiated. *S. longirostris* is basically a shrew of the southern lowlands, although it has been taken in western Virginia (Handley & Patton, 1947). The Clark's Cave collection was referred to *S. cinereus* because of its larger size—somewhat larger than modern *S. cinereus* from the central Appalachians (Table 7)—and the boreal aspect of the accompanying fauna. *Sorex cinereus* was also the commonest long-tailed shrew at New Paris No. 4, Pa., a site of similar age, where the possible presence of *S. longirostris*

did not arise.

The smoky shrew, *S. fumeus*, the commonest *Sorex* in the mountains of western Virginia today, and the commonest long-tailed shrew in the central and southern Appalachians (Smith *et al.*, 1974; Linzey & Linzey, 1971; Handley & Patton 1947), was not common in the deposit. Seven *S. cinereus* were recovered for every *S. fumeus*, and its remains were somewhat less common than those of the arctic shrew (Table 6). *S. fumeus* is common in the deciduous and deciduous/coniferous forests of southeastern Canada and New England. It occurs south in the Appalachian Mountains and flanking plateau areas to northern Georgia (Hall & Kelson, 1959). *S. fumeus* appears to be more dependent on mature forest cover than the two commonest long-tailed shrews from the deposit, *S. cinereus* and *S. arcticus*. Its relative scarcity in mid-Appalachian late Pleistocene deposits suggests more open woodlands in comparison to the dense forest cover that now prevails. Four specimens of *S. fumeus* were trapped by C. O. Handley, Jr. and associates in the Clark's Cave talus in 1974.

Microsorex hoyi (Baird)—Pygmy shrew

MATERIAL: CM 24579. 7 left, 4 right mandibles. MN1 = 7 individuals.

REMARKS: The rarest of the Appalachian long-tailed shrews today, the pygmy shrew appears to have been not as rare in late Pleistocene periglacial sites from eastern North America. It accounted for 6.5% of the long-tailed shrews from Clark's Cave (Table 6), 9.7% from Natural Chimneys, Va., 11.8% from Robinson Cave, Tenn., and 19% from New Paris No. 4, Pa. The latest review (Long, 1972a) lists only 31 modern specimens, from eastern North America, of the races *thompsoni* and *winnemana*. By way of contrast, at least 46 individuals have been recorded in that area from late Pleistocene cave sites: Bootlegger Sink, Pa. (2), New Paris No. 4, Pa. (11), Natural Chimneys, Va. (7), Clark's Cave, Va. (7), Meyer Cave, Ill. (1), Welsh Cave, Ky. (1), and Robinson Cave, Tenn. (17).

Microsorex hoyi exhibits a clear Bergmann's Response. Size increases with latitude. The largest representatives are from northern Canada and Alaska. The smallest races, *montanus*, in the Rocky Mountains, and *winnemana* in the central and southern Appalachian region, mark the southern limits of its Recent range. Surprisingly, measurements of fossil specimens from boreal Wisconsinan faunas in the East agree with those of the Recent *M. h. thompsoni* still in the area. Unlike other insectivores from these deposits which have larger northern races

today, such as *Blarina brevicauda*, measurements show no trend toward larger size in *Microsorex*.

The eastern races of this shrew, *M. h. thompsoni* and *M. h. winnemana*, were originally described as separate species (Baird, 1857; Preble, 1910). Jackson, 1928, recognized only *M. hoyi*, with *thompsoni* and *winnemana* as subspecies. Long, 1972a, regarded *thompsoni* and *winnemana* as closely related to each other and distinct from *M. hoyi*. He grouped these two eastern forms under the species *M. thompsoni*, with *winnemana* as a subspecies. All of the characters differentiating *M. thompsoni* from *M. hoyi* are variable throughout the range of *M. hoyi*. Long, 1972a, and 1974, states that the elevation of *thompsoni* (includes *winnemana*) to species level is tentative and that, "this view needs further study in critical areas."

The apparent small size of these late Wisconsinan fossils suggests that *M. thompsoni* may indeed be a valid species, and that the larger northwestern *M. hoyi* may have spread into eastern Canada from the west during postglacial times. Except for the Gaspé Peninsula, where it is replaced by *M. hoyi*, the northern limit of *M. thompsoni* appears to be defined by the Great Lakes-St. Lawrence waterway, which may have acted as a barrier to its northward spread in postglacial times. Unfortunately, fossil specimens are invariably lower jaws or skull fragments. Taxonomic reviews of living species are based primarily on external characters and complete crania, so that comparison is difficult.

The pygmy shrew, despite its rarity, occurs throughout the Canadian/Hudsonian boreal forest from Alaska to Labrador, and south along the Appalachians in deciduous hardwood forests to the Great Smokies (Long, 1974). Although always found in a forested context and usually fairly close to boreal mesic habitats it may be trapped in such a variety of situations from swamp to dry open country that its presence at the site furnishes no specific ecological

clues (Long, 1972b). There are only two published Recent records from the state of Virginia, both in the Piedmont, well east of the Appalachians proper: one in Fairfax Co., Va., and one at Altavista, Campbell County, 110 km southeast of Clark's Cave, both in deciduous forest (Handley & Patton, 1947). As an example of their modern rarity, Long, 1972a, was able to document only seven specimens south of Maryland. C. O. Handley, Jr., USNM, (pers. comm.) has subsequently acquired three more Virginia specimens.

Blarina brevicauda (Say)—Short-tailed Shrew

MATERIAL: CM 24541: 19 partial skulls, 3 maxillae; 26 left, 22 right mandibles. CM 24578: 67 left, 75 right mandibles; skull fragments. MNI = 97 individuals.

REMARKS: The short-tailed shrew, the commonest one in Virginia today, was also the commonest insectivore from the Clark's Cave deposit. It accounted for 42% of the seven species of shrews recovered from the cave, (42% from Natural Chimneys, Va., and 38.9% from New Paris No. 4, Pa.).

From a paleoenvironmental point of view, osteological remains of this shrew can furnish important clues. Short-tailed shrews vary markedly in size throughout their modern geographic range. Average size increases with latitude. The largest races, *B. b. brevicauda* and *B. b. manitobensis*, are from Minnesota and Manitoba. A smaller race, *B. b. kirtlandi*, occurs in the mid-Appalachians today. A much smaller species, *Blarina carolinensis*, occurs in the southern lowlands of eastern North America. A subspecies, *B. b. churchi*, larger than the mid-Appalachian *B. b. kirtlandi*, is found on the mountain summits of the southern Appalachians—apparently adapted to a cooler environment, a reflection of the same physiological forces that shaped the over-all increase in size with increasing latitude.

The short-tailed shrews from the Clark's Cave deposit were markedly larger than present day mid-

Table 6. Frequencies (%) of species of *Sorex* and *Microsorex* from three late Pleistocene Appalachian cave deposits.¹

Species	Clark's Cave, Va.	Natural Chimneys, Va.	New Paris No. 4, Pa.
<i>Sorex arcticus</i>	12.0 (13)	8.3 (6)	10.3 (6)
<i>Sorex cinereus</i>	62.0 (67)	62.5 (45)	60.3 (35)
<i>Sorex dispar</i>	3.7 (4)	—	6.8 (4)
<i>Sorex fumeus</i>	9.3 (10)	13.9 (10)	1.7 (1)
<i>Sorex palustris</i>	6.5 (7)	5.5 (4)	1.7 (1)
<i>Microsorex hoyi</i>	6.5 (7)	9.7 (7)	19.0 (11)

¹() = MNI.

Table 7. Measurements (in mm) of various species of *Sorex*.

Locality and age	\bar{X}	OR	SD	CV	N
Total mandible length, condyle to anterior point of dentary					
<i>Sorex arcticus</i>					
Clark's Cave, Va., late Pleistocene	9.3	9.1–9.5	----	-----	9
New Paris No. 4, Pa., ¹ late Pleistocene	8.9	8.7–9.3	----	-----	5
<i>S. cinereus</i>					
Pennsylvania, modern ¹	7.28	7.1–7.7	.10	1.37	22
Clark's Cave, Va., late Pleistocene	7.57	7.3–8.0	.21	2.77	18
New Paris No. 4, Pa., ¹ late Pleistocene	7.6	7.2–7.8	.27	3.55	17
<i>S. dispar</i>					
Clark's Cave, Va., late Pleistocene	8.4	8.3–8.4	----	-----	3
New Paris No. 4, Pa., ¹ late Pleistocene	8.2	-----	----	-----	2
<i>S. fumeus</i>					
Clark's Cave, Va., late Pleistocene	9.36	8.9–9.8	----	-----	6
<i>S. palustris</i>					
Clark's Cave, Va., late Pleistocene	10.08	-----	----	-----	1
New Paris No. 4, Pa., ¹ late Pleistocene	9.5	-----	----	-----	1
p4 – m3, antero-posterior crown length ²					
<i>S. arcticus</i>					
Clark's Cave, Va., late Pleistocene	4.64	4.56–4.76	----	-----	7
New Paris No. 4, Pa., ¹ late Pleistocene	4.4	4.2–4.5	----	-----	6
<i>S. cinereus</i>					
Pennsylvania, modern ¹	3.69	3.6–3.9	.07	1.89	20
Clark's Cave, Va., late Pleistocene	3.98	3.6–4.4	.13	3.40	35
New Paris No. 4, Pa., ¹ late Pleistocene	3.9	3.7–4.3	.16	4.09	29
<i>S. dispar</i>					
Clark's Cave, Va., late Pleistocene	4.36	-----	----	-----	1
New Paris No. 4, Pa., ¹ late Pleistocene	4.3	-----	----	-----	1
<i>S. fumeus</i>					
Clark's Cave, Va., late Pleistocene	4.85	-----	----	-----	1
New Paris No. 4, Pa., ¹ late Pleistocene	4.7	-----	----	-----	1
<i>S. palustris</i>					
Clark's Cave, Va., late Pleistocene	5.04	4.9–5.2	----	-----	3
New Paris No. 4, Pa., ¹ late Pleistocene	5.2	-----	----	-----	1

¹Data from Guilday *et al.*, 1964.²Defined as C₁ - M₃ in Guilday *et al.*, 1964 (See Repenning, 1967 for correct terminology).

Table 8. Measurements (in mm)¹ of *Microsorex*.

Taxon and locality	\bar{X}	OR	N
Palatal length			
Recent:			
<i>M. thompsoni</i> ¹	5.60	5.30–5.84	5
<i>M. cf. thompsoni</i> , New Paris No. 3, Pa.	5.24		1
<i>M. t. winnemana</i> ¹	5.25		1
<i>M. h. hoyi</i> ¹	5.67	5.21–6.50	24
<i>M. h. alnorum</i> ¹	5.60	5.54–5.66	6
<i>M. h. eximius</i> ¹	5.86	5.70–5.98	3
<i>M. h. washingtoni</i> ¹	5.56		1
<i>M. h. montanus</i> ¹	5.4	5.26–5.54	3
Late Pleistocene:			
New Paris No. 4, Pa.	5.20	5.1–5.3	4
Welsh Cave, Ky.	5.20		1
Robinson Cave, Tenn.	5.10	4.80–5.30	3
Maxillary breadth			
Recent:			
<i>M. h. montanus</i> ¹	3.9	3.9–4.0	10
<i>M. cf. thompsoni</i> , New Paris No. 3, Pa.	4.17		1
Late Pleistocene:			
New Paris No. 4, Pa.	4.15	4.0–4.3	4
Bootlegger Sink, Pa.	4.1		1
Welsh Cave, Ky.	4.1		1
P4 – M3			
Recent:			
<i>M. cf. thompsoni</i> , New Paris No. 3, Pa.	3.39		1
Late Pleistocene:			
New Paris No. 4, Pa.	3.45	3.4–3.5	4
Robinson Cave, Tenn.	3.5	3.2–3.8	3
Total length of mandible with il			
Recent:			
<i>M. cf. thompsoni</i> , New Paris No. 3, Pa.	8.15		1
Late Pleistocene:			
New Paris No. 4, Pa.	7.97	7.6–8.4	9
Clark's Cave, Va.	8.12	8.05–8.24	3
Total length of dentary			
Recent:			
<i>M. cf. thompsoni</i> , New Paris No. 3, Pa.	6.6		1
Late Pleistocene:			
New Paris No. 4, Pa.	6.5	6.4–6.6	10
Bootlegger Sink, Pa.	6.3		1
Clark's Cave, Va.	6.5	6.3–6.8	7
Robinson Cave, Tenn.	6.5	5.9–7.0	7

¹Measurements from Long, 1972a.

Table 8. Measurements (in mm)¹ of *Microsorex* (continued).

Taxon and locality	\bar{X}	OR	N
Height, ascending ramus			
Recent:			
<i>M. cf. thompsoni</i> .			
New Paris No. 3, Pa.	3.0		1
Late Pleistocene:			
New Paris No. 4, Pa.	2.94	2.9–3.0	9
Bootlegger Sink, Pa.	3.0		1
Clark's Cave, Va.	2.99	2.91–3.10	7
Welsh Cave, Ky.	2.9		1
Robinson Cave, Tenn.	3.2	2.9–3.5	20
p4 – m3			
Recent:			
<i>M. cf. thompsoni</i> ,			
New Paris No. 3, Pa.	3.39		1
Late Pleistocene:			
Bootlegger Sink, Pa.	3.49		1
Clark's Cave, Va.	3.51	3.39–3.69	5
Welsh Cave, Ky.	3.6		1
m1 – m3			
Recent:			
<i>M. cf. thompsoni</i> ,			
New Paris No. 3, Pa.	2.91		1
Late Pleistocene:			
New Paris No. 4, Pa.	2.86	2.8–3.1	8
Bootlegger Sink, Pa.	2.91		1
Clark's Cave, Va.	2.97	2.8–3.2	8
Welsh Cave, Ky.	2.8		1
Robinson Cave, Tenn.	2.9	2.8–3.1	12

¹Measurements from Long, 1972a.

Appalachian specimens, in keeping with the boreal aspect of the deposit. Four of the five cranial measurements taken average larger than those of *B. b. brevicauda* from Minnesota (Table 9). Maxillary breadth of 15 Clark's Cave skulls average only 0.14 mm smaller than the type and allotype of *B. b. Manitobensis* (Anderson, 1947:23), the largest modern subspecies. Three specimens (of 15) exceeded this. The total length of the lower jaw averaged 8.6% larger, and the length of the lower toothrow (p4-m3) 7.6% larger than modern *B. b. kirtlandi*. The Clark's Cave fossil *Blarina* are comparable in size to the largest living subspecies and to the larger of the two size groups from New Paris No. 4, Pa.

The Clark's Cave sample, in addition to being composed of specimens much larger than those now

in the area, appears to be homogeneous, i.e., not racially mixed. Total variation of the length of the lower jaw amounted to only 11% (% increase of largest to smallest), with a low coefficient of variation of 3.00, comparable to that of a Recent Pennsylvania sample of *B. b. kirtlandi* (Guilday *et al.*, 1964:151). In contrast, in the New Paris No. 4, Pa., *Blarina* sample, composed of a mixture of large late Pleistocene and smaller Recent specimens, total variation of that measurement rose to 20%, with a coefficient of variation of 5.74. At Meyer Cave, Ill., where the *Blarina* were markedly heterogeneous, a mixture of large *B. b. brevicauda* and smaller *B. b. cf. kirtlandi*, total variation was 25%, over twice that shown by the Clark's Cave sample.

This is one of the few species in the deposit yield-

Table 9. Measurements (in mm) of *Blarina brevicauda*, various localities.

Locality	\bar{X}	OR	SD	CV	N
Maxillary breadth					
<i>Recent:</i>					
Minnesota ¹	8.4	8.0–9.2	0.35	4.13	21
Pennsylvania ¹	7.8	7.0–8.3	0.22	2.80	77
Cowpasture River valley, Bath Co., Va. Elevation 440–485 m USNM 489606–489610, 489704–489714	7.6	7.2–7.8	0.18	2.37	16
Warm Springs Mountain, Bath Co., Va. Elevation 644–1106 m USNM 489880–489884	7.8	7.5–8.0	—	—	5
White Sulphur Springs, Greenbriar Co., W. Va. ²	7.66	7.2–8.02	—	—	10
Pisgah Forest, Transylvania Co., N. C. ²	7.53	7.2–8.0	—	—	10
<i>Late Pleistocene</i>					
New Paris No. 4, Bedford Co., Pa. ¹	8.50	8.1–8.9	—	—	2
Natural Chimneys, Augusta Co., Va. ¹	8.31	8.0–8.7	—	—	4
Clark's Cave, Bath Co., Va.	8.66	8.2–9.1	0.26	3.06	15
Total length, mandible (including incisor)					
<i>Recent:</i>					
Minnesota ¹	16.2	14.9–17.6	0.67	4.13	19
Pennsylvania ¹	15.15	14.6–16.0	0.32	2.09	17
Cowpasture River valley, Bath Co., Va. (data above)	15.3	14.8–15.9	0.16	1.04	16
Warm Springs Mountain, Bath Co., Va. (data above)	15.2	14.6–15.6	—	—	5
<i>Late Pleistocene:</i>					
New Paris No. 4, Bedford Co., Pa. ¹	15.3	13.8–17.2	0.88	5.74	29
Clark's Cave, Bath Co., Va.	16.6	15.5–18.4	0.50	3.00	52
Length of dentary (from condyle)					
<i>Recent:</i>					
Cowpasture River valley, Bath Co., Va. (data above)	12.4	11.9–13.1	0.47	3.79	15
Warm Springs Mountain, Bath Co., Va. (data above)	12.2	11.9–12.4	—	—	5
<i>Late Pleistocene:</i>					
Clark's Cave, Bath Co., Va.	13.3	12.3–15.2	0.54	4.05	60

¹Data from Guilday *et al.*, 1964.²Data from Ray, 1967, Table 2.

Table 9. Measurements (in mm) of *Blarina brevicauda*, various localities (continued).

Locality	\bar{X}	OR	SD	CV	N
p4 – m3, Antero-posterior Crown Length ³					
<i>Recent:</i>					
Minnesota ¹	6.29	5.8–6.6	0.19	3.02	20
Pennsylvania ¹	6.06	5.7–6.3	0.19	3.13	24
Cowpasture River valley, Bath Co., Va. (data above)	6.1	5.9–6.3	0.22	3.60	16
Warm Springs Mountain Bath Co., Va. (data above)	6.2	6.0–6.3	-----	-----	5
White Sulphur Springs, Greenbrier Co., W. Va. ²	5.85	5.48–6.19	-----	-----	10
Pisgah Forest, Transylvania Co., N. C. ²	5.78	5.47–5.98	-----	-----	10
<i>Late Pleistocene:</i>					
New Paris No. 4, Bedford Co., Pa. ¹	6.14	5.5–6.8	0.39	6.48	36
Natural Chimneys, Augusta Co., Va. ¹	6.43	6.2–6.6	0.13	2.02	9
Clark's Cave, Bath Co., Va.	6.56	6.2–6.9	0.14	2.13	57
Width, mandibular condyle					
<i>Recent:</i>					
Minnesota ¹	4.16	3.9–4.6	0.19	4.56	22
Pennsylvania ¹	3.85	3.7–4.1	0.13	3.37	24
Cowpasture River valley, Bath Co., Va. (data above)	3.89	3.7–4.2	0.18	4.62	16
Warm Springs Mountain, Bath Co., Va. (data above)	3.89	3.8–4.0	-----	-----	5
<i>Late Pleistocene:</i>					
New Paris No. 4, Bedford Co., Pa. ¹	3.91	3.3–4.5	0.30	7.67	37
Clark's Cave, Bath Co., Va.	4.01	3.49–4.65	0.20	5.03	13

¹Data from Guilday *et al.*, 1964.²Data from Ray, 1967, Table 2.³Defined as C₁–M₃ in Guilday *et al.*, 1964. (See Repenning, 1967 for terminology).

ing clues to the minimum date of deposition. *Blarina* occurred continuously from boreal times to the present in the area. During this time span it diminished in size. If deposition had continued undiminished, remains of this shrew would have been expected to reflect this. They did not. From an inspection of the measurements in Table 9 and the low

coefficient of variation from the Clark's Cave sample, it is apparent that the deposit was composed primarily of large individuals—the minimum measurements recorded exceed the average of Recent *B. b. kirtlandi*. This size difference is clearly brought out by comparing the measurements of the Clark's Cave *Blarina* sample with those from Recent examples

from the Cowpasture River valley taken by Charles O. Handley, Jr. and his students (Table 9). It would appear that all short-tailed shrews, and by extension the bulk of the deposit, accumulated prior to any diminution in size, and that deposition therefore ceased at that spot by the close of late Pleistocene times, or if deposition continued to occur, it was not on a sustained basis.

The large size of the short-tailed shrew remains is indicative of more boreal conditions, but its wide choice of habitats, occupying practically all terrestrial habitats within the forested East, are too broad to provide any specific ecological clues. Short-tailed shrews range north to the shores of James Bay.

Remains of this shrew were conspicuously absent from the lower levels of the stratified New Paris No. 4, Pa., deposit. These lower levels produced only boreal mammals, and it appears that at that site, the short-tailed shrew was absent during full glacial times, becoming common only with the return of more temperate conditions. But it may have been present at that time at Clark's Cave, two degrees latitude to the south. Further collections may clarify the situation.

Family: Talpidae—Moles

Parascalops breweri (Bachman)—Hairy-tailed Mole

MATERIAL: CM 24537. 2 partial skulls; 8 left, 7 right mandibles; 11 left, 12 right humeri. MNI = 12 individuals.

Scalopus aquaticus (Linnaeus)—Eastern Mole

MATERIAL: CM 24539. 1 partial right mandible, no dentition; 1 left humerus. MNI = 1 individual.

Condylura cristata (Linnaeus)—Star-nosed Mole

MATERIAL: CM 24538. 12 left, 4 right partial mandibles; 11 left, 13 right humeri; 1 rostrum. MNI = 13 individuals.

REMARKS: Moles (0.9% of all terrestrial mammals) were rare in the deposit. Their secretive habits protect them from aerial predation. The eastern mole, *Scalopus*, was represented by a single individual. The hairy-tailed mole, *Parascalops* (46%), and the star-nosed mole, *Condylura* (50%), were present in equal numbers. This is in striking contrast to the situation at Sheep Rock Shelter, Pa., 300 km north of Clark's Cave, where *Scalopus* accounted for 89% of all moles, *Condylura* 9%, and *Parascalops* but 2.8%. The modern ecological situation is much the same at both sites, a narrow intermontane flood plain between high, parallel, oak-forested ridges in the Atlantic drainage. The high numbers of *Scalopus* at Sheep Rock, compared with the situation at Clark's Cave is, we believe, due to the relative age of the two

sites. Sheep Rock Shelter is a Recent owl roost uninfluenced by late Pleistocene climatic changes.

Both *Parascalops* and *Condylura* occur in western Virginia today (Handley & Patton, 1947). They probably do not occur as low as Clark's Cave or, if so, rarely. *Scalopus*, however, should occur in the extensive flat flood plain of the Cowpasture River above and below the site within cruising range of the Clark's Cave owl population. Its relative rarity in the fossil deposit is an indication of the predominantly boreal conditions reflected by the fossil assemblage. The fact that *Scalopus* was taken in such large numbers relative to *Parascalops* and *Condylura* at Sheep Rock indicates that the eastern mole was as susceptible to owl predation as the other two species of moles. Its scarcity in the Clark's Cave deposit must reflect the true picture at the time of deposition. Moles were relatively more common at Sheep Rock (12% of mammals against 0.9% at Clark's). This reflects differences in excavation technique. The total recovery attempted at Clark's Cave resulted in larger numbers of other small mammals from the sample.

Parascalops and *Condylura* have similar modern ranges in the Appalachian Mountains and adjacent plateau country of eastern North America north to the southern portion of the Canadian Shield. *Parascalops* is found no farther north than Maine. *Condylura* ranges north to James Bay and southern Labrador. Both had more extensive ranges during the boreal phase of the Wisconsinan. *Parascalops* has been reported from Robinson Cave in central Tennessee, and *Parascalops* and *Condylura* from Crankshaft Pit in the Ozark Highlands of southeastern Missouri. The range of *Scalopus*, on the other hand, is austral, including all the southern and central United States north to Minnesota, Michigan, and Massachusetts. It enters the Appalachians only in areas where it can follow the low altitude flood plains and rivers that traverse the mountain ridges.

The one *Scalopus* humerus measures 14.8 mm in length and 12.5 mm in width, well within the range of *S. a. aquaticus*, the race living in the state today (Guilday, 1961a:117, Table 1, for comparative measurements).

Adult males of both the star-nosed and the hairy-tailed moles are larger than females. The Clark's Cave samples are too small to adequately express the true extent of variation, but they do suggest sexual size differences as in the living animals. This is reflected by the slightly larger coefficient of variation of p4-m3 of the Clark's Cave *Condylura*, com-

Table 10. Measurements (in mm) of *Condylura cristata* and *Parascalops breweri*.

Locality and age	\bar{X}	OR	SD	CV	N
<i>Condylura cristata</i>					
Alveolar length p4 - m3					
<i>Recent:</i>					
Pennsylvania, males (CM 23864-71, 23874-5, 23877-80)	6.3	6.1-6.6	0.15	2.37	14
<i>Late Pleistocene:</i>					
Clark's Cave, Va.	6.8	6.5-7.2	0.23	3.37	16
Maximum length, humerus					
<i>Recent:</i>					
Pennsylvania, males	13.0	12.8-13.2	—	—	6
<i>Late Pleistocene:</i>					
Clark's Cave, Va., females?	13.1	12.8-13.4	—	—	11
Clark's Cave, Va., males?	13.9	13.8-14.3	—	—	8
Clark's Cave, Va., sexes combined	13.4	12.8-14.3	0.46	3.46	19
<i>Parascalops breweri</i>					
Maximum length, humerus					
<i>Late Pleistocene:</i>					
Clark's Cave, Va., males?	14.6	14.0-15.2	—	—	10
Clark's Cave, Va., females?	13.4	13.2-13.7	—	—	5
Clark's Cave, Va., sexes combined	14.2	13.2-15.2	0.65	4.58	15

pared with the same measurement in a sample of Recent males, and in the bimodal distribution of the total length of *Condylura* humeri. The Clark's Cave *Condylura* humeri fell into two size classes, with no overlap in their observed ranges (Table 10): females? 12.8-13.4, males? 13.8-14.3. An alternate explanation, that the Clark's Cave sample is composed of two intermingled populations, a larger late Pleistocene and a smaller Recent form, was rejected because a similar situation could not be demonstrated in those species, *Blarina brevicauda*, for example, where a significant sexual size difference does not occur.

Humerus length of six Recent male *Condylura* (Table 10), the larger sex, fell within the range of the Clark's Cave presumed females and were significantly smaller than those of presumed males from the deposit. The Recent males averaged some 6.5% smaller than the Clark's Cave males?, suggesting that the late Pleistocene population, as at New Paris No. 4, Pa., was indeed larger in body size than its modern regional counterpart.

In the case of *Parascalops*, little, if any, size difference can be shown. Sexual size differences are suggested by the relatively broad observed range of

humeri (Table 10), but the sample is too small to be other than suggestive.

Order: Chiroptera—Bats

Family: Vespertilionidae—Evening Bats

At least 1,554 individual bats were represented, and their remains formed 36% of the total mammalian assemblage at the site. Bats are not usually represented in raptor prey. Their high numbers at Clark's Cave reflected the presence of a large bat colony in the cave itself. Gillette and Kimbrough (1970:265) cite instances of bat predation by raptors, "groups of hawks or falcons working together in a small area with devastating effectiveness on emerging or returning colonies." The nocturnal feeding habits of bats and owls bring them into contact with greater frequency, and owl predation on bats is well-documented (Hall & Blewett, 1964). The roost site, ideal for birds of prey, is too shallow and exposed to have served as a hibernaculum, and most of the excavated bat bones are presumed prey items derived from the large bat population deep in the cave itself.

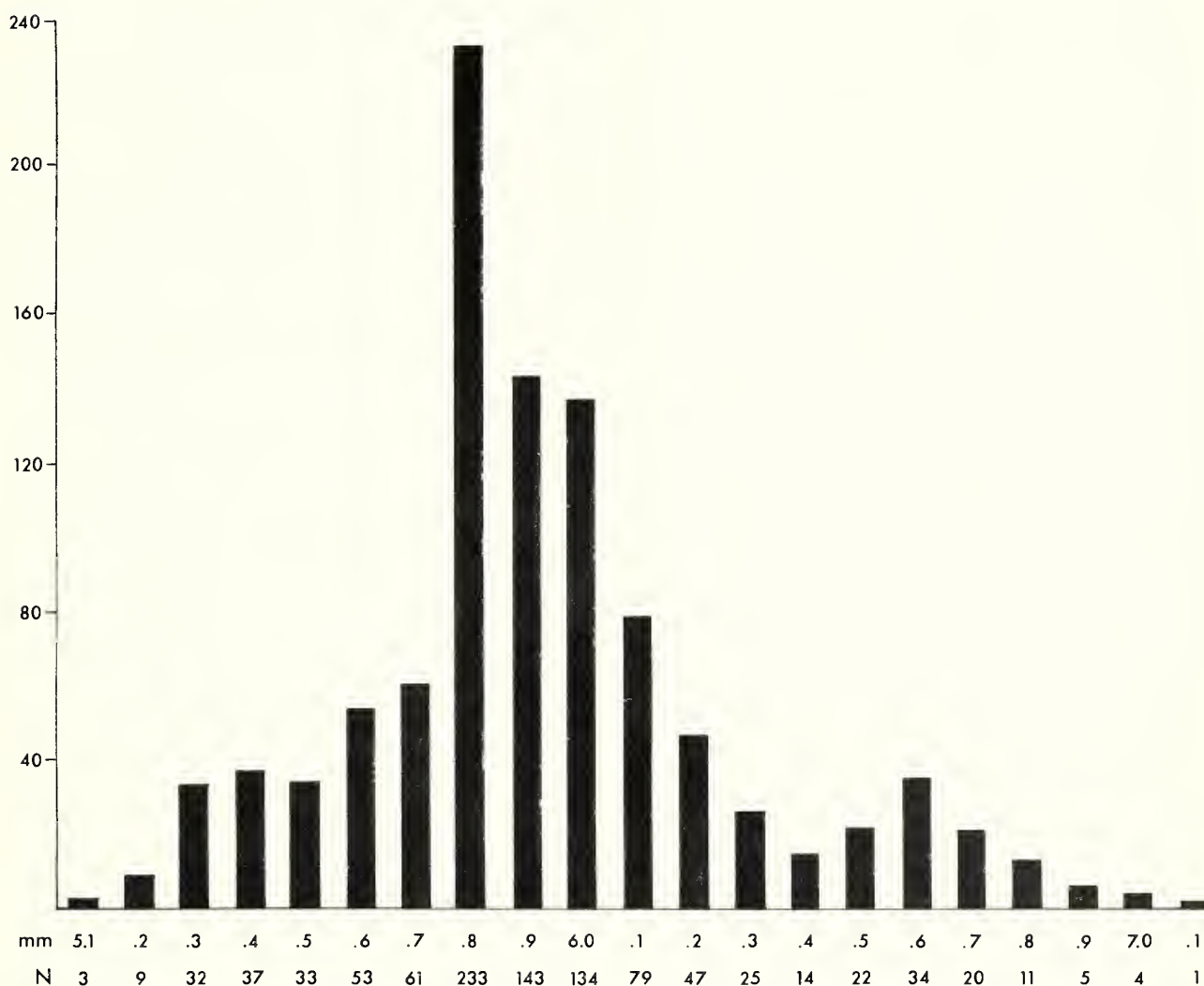
Genus *Myotis* Kaup—Little Brown Bats

MATERIAL: CM 24599-24619. 2,309 whole or partial mandibles.

1,000 of the most complete are grouped in lots according to alveolar length of lower tooththrow, c-m3, in 0.1 mm increments. Additional material, unmeasured mandibles, skull fragments etc., under CM 24626-24628. A minimum of 877 *M. lucifugus*, *M. sodalis*, or *M. keenii* based upon 76% of all *Myotis*. A minimum of 138 *M. cf. leibii* based upon 12% of all *Myotis*. A minimum of 138 *M. cf. grisescens* based upon 12% of all *Myotis*.

REMARKS: All identifications are based upon lower jaws. Alveolar length of lower tooththrow c-m3

of 1,000 specimens is shown in the graph in Fig. 16. The Clark's Cave *Myotis* sample is composed of three subgroups based upon size. A trimodal curve results with modes at 5.4, 5.8, and 6.6 mm. These could be related to modern eastern North American species. The smaller group, mode 5.4 mm, about 12% of the *Myotis* in the sample, is *Myotis cf. leibii*, Leib's bat. Although never a common species, Leib's



Myotis, all species, Clark's Cave, Bath County, Virginia, alveolar length c1 - m3

N = 1,000 (489 left; 511 right) lower jaws. Ordinate = number of individuals

Fig. 16. Histogram. Measurements in millimeters of mandibles of various species of bats, *Myotis*, from Clark's Cave, Bath County, Virginia.

bat is broadly distributed in the East from Maine and southern Quebec south to western Virginia (Hall & Kelson, 1959). Not listed as a member of the fauna of Virginia by Handley & Patton, 1947, it has subsequently been reported from Millboro Cave, Bath County, and Hupman's Saltpeter Cave, 750 m elevation, in neighboring Highland County (Johnson, 1950), and present but rare, in Starr Chapel and Porter's Caves, Bath County (Holsinger, 1964). Four specimens were netted at entrance No. 3 of Clark's Cave in August, 1974, by C. O. Handley, Jr.

The larger subgroup, mode 6.6 mm, estimated as 12% of all *Myotis*, is *M. cf. grisescens*, the gray bat. This bat has been reported only in extreme southwestern Virginia, Grigsby Cave, in Scott County (Holsinger, 1964). It has been recorded as a fossil north and east of its present range from Cumberland Cave, Md., and Organ-Hedricks, Windy Mouth, and Patton Caves, W. Va. (Handley, 1956a:251). These records, coupled with the evidence of a sizeable former population in Clark's Cave, suggest a range shift to the southwest since late Pleistocene times.

By far the bulk of the *Myotis*, about 75%, fell within an intermediate range. Inspection of this curve, mode 5.8 mm, indicates that unlike the other two, which appear symmetrical, it is strongly skewed to the left. There are at least two and possibly three species of *Myotis* represented here: *M. lucifugus*, the little brown bat; *M. sodalis*, the social bat; and *M. keenii*, Keen's bat. At the present time, *M. lucifugus* is the commonest northeastern cave bat, *M. keenii* is moderately common, and *M. sodalis* is uncommon. During the years 1946-1951, six *M. lucifugus* were collected for each *M. keenii* in Pennsylvania (Roberts & Early, 1952). There is some evidence that *M. keenii* may have been relatively more common during the late Pleistocene in Pennsylvania, at least. New Paris sinkhole No. 4 yielded the remains of 302 *M. keenii*, but only 225 *M. cf. lucifugus* or *sodalis* (Guilday *et al.*, 1964:151). The fact that the frequency curve is skewed towards the small end of the scale suggests that the commonest component species was probably *M. lucifugus* (or *M. sodalis*) and that the larger *M. keenii* was the minority species. No attempt was made to assign a specific identification to particular specimens because of the extensive overlap in measurements in modern samples and the poor state of preservation of the fossils. Holsinger, 1964, records *M. keenii*, *M. lucifugus*, and *M. sodalis* from Bath County caves.

Pipistrellus subflavus (F. Cuvier)—Pipistrelle Bat

MATERIAL: CM 24620. 26 left, 19 right mandibles. MNI = 26 individuals.

REMARKS: Pipistrelles comprised only 1.2% of the total number of bats recovered. In contrast, they formed 53% (45 out of 84 bats) of a mist-net sampling run for three hours at entrance no. 3 of Clark's Cave in August, 1974. Alveolar length c-m3, mm followed by (N): 4.5(1), 4.6(8), 4.7(5), 4.8(16), 4.9(3), 5.0(5), 5.1(1).

Eptesicus fuscus (Palisot de Beauvois)—Big Brown Bat

MATERIAL: CM 24624, 24625. 341 left, 363 right mandibles, partial skulls and fragments. MNI = 363 individuals.

REMARKS: The big brown bat is a common species at the cave today. It comprised 15% (13 out of 84) of the mist-netted bats, August, 1974.

Lasiurus cf. borealis (Muller)—Red Bat

MATERIAL: CM 24621. 3 left, 2 right mandibles. MNI = 3 individuals.

REMARKS: Although this tree bat is one of the commonest of eastern North American bats, it is not normally a cave-frequenting species and would not be captured with any frequency at the cave entrance by birds of prey. Alveolar length c-m3, mm followed by (N): 5.1(1), 5.3(1), 5.8(2), 5.9(1).

Plecotus E. Geoffroy Saint Hilaire—Big-eared Bats

MATERIAL: CM 24622. 9 left, 7 right mandibles. MNI = 9 individuals.

REMARKS: Two Recent species of big-eared bats have been reported from Virginia, *P. rafinesquii* Lesson and *P. townsendii* Cooper. *P. rafinesquii* is a bat of the southeastern United States and the Mississippi Valley as far north as Ohio. The sole Virginia record is from Dismal Swamp on the coastal plain (Handley, 1959:161). It has been collected in the Appalachians just west of the state, however, in eastern Tennessee, Kentucky, and West Virginia (Collison Cave, Nicholas Co., Handley, 1959:165).

The only Recent record of a big-eared bat from the mountainous western portion of the state is of *P. townsendii*, the western big-eared bat. There is a thriving population of this bat in the central Appalachians, separated by some 960 km from the Ozark Mountain segment of its range. According to Handley they have been reported from at least 19 caves from the West Virginia highlands within an area 48 km wide and 64 km long (*ibid*:202) north of Clark's Cave, with an isolated station 240 km southwest in Tazewell County, Va. Holsinger, 1964, reports *P. town-*

sendii from caves of over 600 m elevation from Highland and Bath counties, Virginia.

The Clark's Cave specimens, fragmentary mandibles, could have been either species. Mandibles of a third species, the extinct *P. alleganiensis* described from the mid-Pleistocene Cumberland Cave deposit, are not distinguishable from modern species of *Plecotus*. But Cumberland Cave clearly antedates the Clark's Cave deposit (Gidley & Gazin, 1938). Bats of the genus *Plecotus* have also been reported from Frankstown Cave, a Pleistocene fissure deposit in the Ridge and Valley section of central Pennsylvania (Guilday, 1961b).

Handley, 1959, regards the disjunct Appalachian distribution of *P. townsendii* as a relict of a more extensive past distribution. Its isolation is reflected in its recognition as a distinct subspecies, *P. t. virginianus*.

The big-eared bat population of Clark's Cave was never a large one. The few remains from the fossil deposit, representing only 9 individuals, or 0.6% of the fossil bat fauna, may have been from itinerant individuals.

Order: Lagomorpha—Rabbits, Hares, Pikas

Family: Leporidae—Rabbits and Hares

Sylvilagus cf. *transitionalis* (Bangs)—

New England Cottontail

MATERIAL: CM 24591. Partial left innominate, distal end of left femur. MNI = 1 individual.

REMARKS: The minimum number of all leporids from Clark's Cave is 27 (1% of all terrestrial mammals). All but one, based on the two fragments listed above as *S. transitionalis*, are referred to snowshoe hare. The *S. transitionalis* bones are small (Table 11), too small for snowshoe hare or common cottontail *S. floridanus*. The diagnostic supraorbital processes were not preserved, so the identification, based solely on size, is provisional.

Handley & Patton, 1947:189, state that *S. transitionalis* is found at higher elevations throughout the mountainous portions of the state, probably not below 750 m elevation. It is sympatric with *Lepus americanus* in Virginia today. Bailey, 1946:282, specifically lists Bath County in the modern range.

Fossil or subfossil remains have also been reported from New Paris No. 4, Pa., and Ladds Quarry, Ga.

Lepus americanus Erxleben—Snowshoe Hare

MATERIAL: CM 24590. 18 left, 14 right premaxillae (14 retaining first incisors); 32 isolated first upper incisors; 2 left, 2 right frontals; 10 left, 8 right maxillae; 1 occipital; 17 left, 13

right mandibles; 9 atlas vertebrae; 21 left, 15 right scapulae; 12 left, 10 right humeri; 14 ulnae; 4 radius; 21 right, 6 left innominate; femora—16 proximal, 13 distal ends, 1 complete; 15 left, 8 right tibia; 15 left, 17 right calcanea. MNI = 23 individuals.

REMARKS: The snowshoe hare does not occur in the Cowpasture River valley or the surrounding hills today. Handley & Patton (1947:186) state that the snowshoe hare probably occurred at one time throughout the mountainous areas of the state at higher elevations. "Now known to occur only in Highland County, where it is uncommon . . . restricted to areas of spruce and fir, found in open woods and thickets."

Characters differentiating *Lepus* from *Sylvilagus* included shape of the supraorbital processes, the occipital, the posterior margin of incisive foramen, the rugosity of the zygoma, and the relative slenderness of shafts of humerus, femur, and tibia.

Although most of the lagomorph material was so fragmentary that specific, even generic, identification was not possible, all, with the exception of two elements identified as New England cottontail, CM 24591, are referred to *Lepus americanus* for the following reasons: (1.) All preserved diagnostic parts were *Lepus*; (2.) Measurements average slightly larger than late Pleistocene specimens of *L. americanus* from New Paris No. 4, Pa.

The complicating factor in identification is that gross size cannot be used in separating *L. americanus* from *Sylvilagus floridanus*. Modern *L. a. virginianus* from the central Appalachians is easily distinguished from *Sylvilagus* by virtue of its larger size, but late Pleistocene populations of *L. americanus*, like those at New Paris No. 4, Pa., are as small as modern *Sylvilagus* from the same area. They are indistinguishable on the basis of size alone.

Order: Rodentia—Rodents

Family: Sciuridae—Squirrels

Tamias striatus (Linnaeus)—Eastern Chipmunk

MATERIAL: CM 24533. 22 left, 24 right whole or partial mandibles; 5 left, 4 right maxillae. MNI = 24 individuals.

REMARKS: The eastern chipmunk is common throughout the state at all altitudes and in all types of brushy or forested situations today (see Handley & Patton, 1947 for exceptions). It is also common in the Clark's Cave deposit, comprising 22% of the eight species of sciurids from the deposit.

The Clark's Cave sample is composed of chipmunks larger in size than present mid-Appalachian forms (Table 12). They agree in size with both the late Pleistocene sample from New Paris No. 4, Pa.,

and the largest living subspecies, *T. s. pipilans* (Table 12).

Tamias striatus from the Appalachians exhibits a negative Bergmann's Response. It *increases* in size with *decreasing* latitude. Specimens from Quebec

at the northern extremity of its northeastern range average 5% smaller in total length of skull than specimens from western North Carolina (Table 12). Individuals of *T. s. pipilans* from Louisiana, the largest subspecies, may be as much as 12.5% larger

Table 11. Measurements (in mm) of *Lepus americanus*, *Sylvilagus floridanus* and *Sylvilagus transitionalis*.

Locality	\bar{X}	OR	N
Distal width of humerus			
<i>Lepus americanus</i> , Recent, Pa.	10.1	9.5–10.5	6
<i>Lepus americanus</i> , New Paris No. 4, Pa. late Pleistocene	8.3	7.5–9.1	28
<i>Lepus americanus</i> , Clark's Cave, Va. late Pleistocene	8.8	8.3–9.5	18
<i>Sylvilagus floridanus</i> , Recent, Pa.	8.1	7.7–8.6	10
<i>Sylvilagus transitionalis</i> , Recent, Mass.	7.5	7.3–7.7	2
Anterior-posterior diameter of acetabulum			
<i>Lepus americanus</i> , New Paris No. 4, Pa., late Pleistocene	7.8	7.0–8.4	20
<i>Lepus americanus</i> , Clark's Cave, Va. late Pleistocene	7.95	7.4–8.9	16
<i>Sylvilagus floridanus</i> , Recent, Pa.	8.2	7.5–9.1	9
<i>Sylvilagus transitionalis</i> , Recent, Mass.	7.7	7.0–8.4	2
<i>Sylvilagus</i> cf. <i>transitionalis</i> , Clark's Cave, Va., late Pleistocene	6.5	-----	1
Distal width of femur			
<i>Lepus americanus</i> , Recent, Pa.	15.4	14.8–16.4	7
<i>Lepus americanus</i> , New Paris No. 4, Pa. late Pleistocene	13.2	12.4–14.3	20
<i>Lepus americanus</i> , Clark's Cave, Va. late Pleistocene	13.4	12.3–14.5	11
<i>Sylvilagus floridanus</i> , Recent, Pa.	13.4	12.8–13.8	10
<i>Sylvilagus transitionalis</i> , Recent, Mass.	12.0	11.7–12.3	2
<i>Sylvilagus transitionalis</i> , Clark's Cave, Va., late Pleistocene	11.5	-----	1
Distal width of tibia			
<i>Lepus americanus</i> , Recent, Pa.	13.5	12.4–14.5	7
<i>Lepus americanus</i> , New Paris No. 4, Pa., late Pleistocene	11.2	11.0–11.5	9
<i>Lepus americanus</i> , Clark's Cave, Va., late Pleistocene	11.7	11.0–12.8	18
<i>Sylvilagus floridanus</i> , Recent, Pa.	11.2	11.0–11.6	5
<i>Sylvilagus transitionalis</i> , Recent, Mass.	10.3	-----	1

Measurements by W. Pollock and A. Guilday.

Specimens examined:

Lepus americanus, Recent, Pa.: CM 2212, 2211, 2213, 2214, 2215, 2217, 2216, 33286, 33284, 33285, G-644; New Paris No. 4, Pa., late Pleistocene: CM collections; Clark's Cave, Va., late Pleistocene: CM 24590.

Sylvilagus floridanus, Recent: CM 27007, 27008, 27010, 27012, 7951, 7952, 8363, 10673, 19365, 35790, 10137, 7651, G-8.

Sylvilagus transitionalis: no number, Guilday collection, Mass.; Clark's Cave, Va., late Pleistocene: CM 24591.

in total length of skull (USNM 28459, Ray, 1965: 1020) than average Quebec specimens.

Unfortunately, comparable measurements could not be taken from the fragmentary Pleistocene specimens, but those from Clark's Cave average 8% larger in alveolar length of lower tooththrow than modern Pennsylvania specimens of *T. s. fisheri*. Although the eastern chipmunk does become smaller toward the north in the eastern portion of its range, it becomes larger at all latitudes toward the west. It is possible that the superior size of the late Pleistocene *T. striatus* from the mid-Appalachians may be a reflection of the same environmental conditions that accounted for the influx of so many midwestern forms into the Appalachians at that time.

At Clark's Cave and Natural Chimneys, Va., remains of nocturnal, arboreal flying squirrels exceeded those of terrestrial, diurnal chipmunks 2/1 and 3/1 respectively. At New Paris No. 4, Pa., the reverse was true. Chipmunk remains outnumbered those of flying squirrels by 2/1. Marked changes in the relative percentages of species from two or more sites sam-

pling the same temporal fauna in the same general geographic area, in this case the mid-Appalachians, reflect either differing habitats, predator preferences, or methods of deposition. The Clark's Cave and Natural Chimneys deposits were formed largely by owls, which accounted for a large number of nocturnal flying squirrels in comparison with the number of diurnal chipmunks. At New Paris No. 4, Pa., animals were trapped in an open tumble-in sinkhole, resulting in higher numbers of terrestrial, as opposed to arboreal, forms. Predator bias was not a factor at New Paris No. 4, so nocturnal forms were not selected, as in the case of the owl roost sites.

Eutamias minimus (Bachman)—Least Chipmunk

MATERIAL: CM 24532. 2 left mandibles with full dentition; 1 left, 1 right mandible with p4-m1. MNI = 3 individuals.

REMARKS: The least chipmunk has not previously been reported from the Appalachians, either fossil or Recent. It occurs in western and central North America, usually in open to brushy, boreal, coniferous forest situations, and reaches its greatest

Table 12. Measurements (in mm) of *Tamias striatus*.

Locality and taxa	\bar{X}	OR	SD	CV	N
Alveolar length, p4 – m3					
<i>Recent:</i>					
<i>T. striatus pipilans</i> ¹	6.76	6.3–7.4	0.30	4.40	19
New Paris No. 2, Pa. (1,875 yrs. B.P.)	6.28	5.8–6.8	0.18	2.86	114
<i>Late Pleistocene:</i>					
New Paris No. 4, Pa. (11,300 yrs. B.P.)	6.74	6.3–7.1	0.20	6.67	30
Hartman's Cave, Pa. ¹	6.90	6.2–7.7	0.42	6.11	9
Clark's Cave, Va.	6.81	6.5–7.3	0.21	3.08	28
Robinson Cave, Tenn.	7.5	7.3–7.8	—	—	2
Total length of skull					
<i>Recent:</i>					
<i>T. s. quebecensis</i> , Quebec ³ 48° 30' N. lat.	39.1	37.4–40.0	—	—	4
<i>T. s. lysteri</i> , Ontario ² 43° 30' N. lat.	39.4	38.0–40.1	—	—	7
<i>T. s. fisheri</i> , N.Y. ² 41° N. lat.	40.1	38.8–41.0	—	—	10
<i>T. s. striatus</i> , N.C. ² 34° N. lat.	41.1	39.8–42.6	—	—	11
<i>Pleistocene:</i>					
<i>T. aristus</i> , Ga. ¹ 34° N. lat.	52.7	—	—	—	1

Measurements from Ray, 1965¹; Howell, 1929²; Cameron, 1950³.

abundance in open, sandy, pine and spruce parklands. It is not found in the United States east of Wisconsin. But north of the Great Lakes it occurs across the southern half of Ontario east to extreme western Quebec, 800 km north of Clark's Cave (Banfield, 1974), as shown in Fig. 17.

Identification, based upon dentitions, both lower and (Back Creek Cave No. 2, Va.) upper, is firm to genus. Referral to *E. minimus* is based on small size, geographic proximity, and ecological probability.

The eastern chipmunk (*Tamias*), an inhabitant of deciduous forest and brushland, and the least chipmunk (*Eutamias*) coexist today in a broad area of east-central Canada extending from southern Manitoba and northern Wisconsin and Minnesota toward the east and north of the Great Lakes for 650 km across the southern half of Ontario (Fig. 18). Where the two occur in the same general area, *Tamias* prefers deciduous, *Eutamias* coniferous, forest situations. Their remains also have been found together at the 7,000 to 7,500-year B.P. levels at

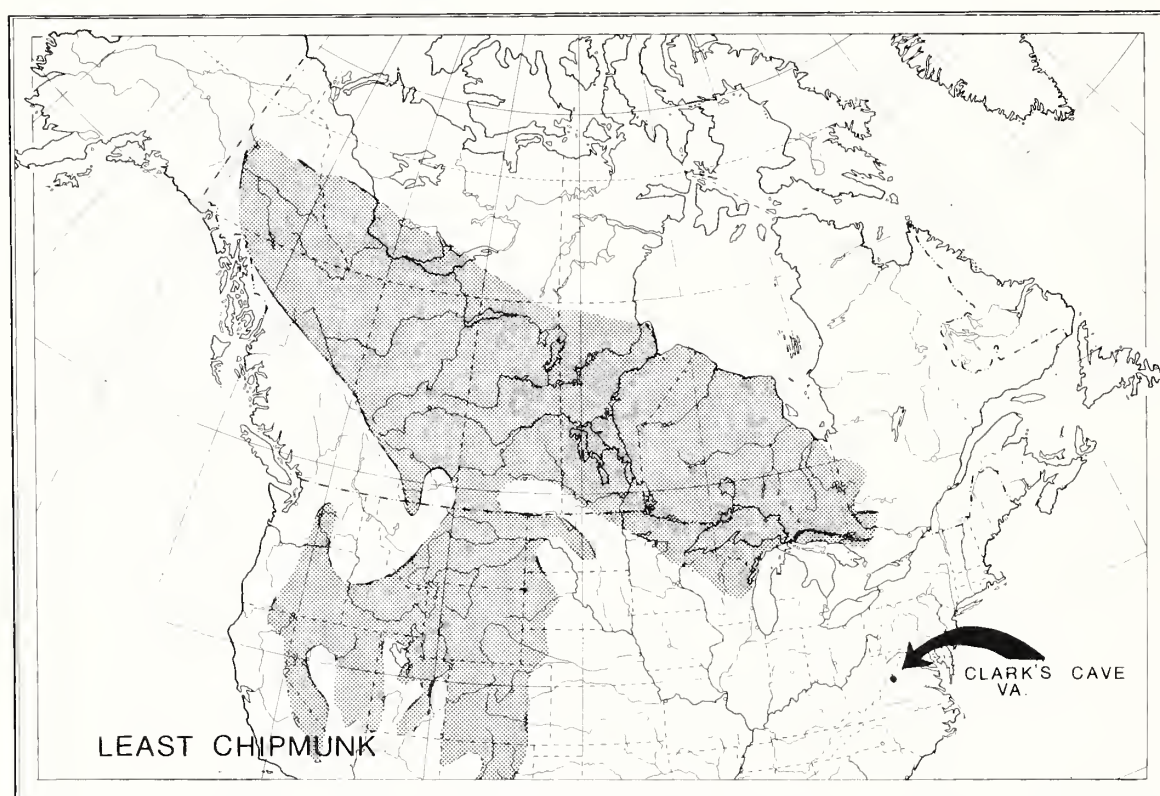


Fig. 17. Modern range of least chipmunk, *Eutamias minimus* (Bachman), adapted from Hall & Kelson, 1959. Present in Clark's Cave local fauna.

Table 13. Measurements (in mm) of *Eutamias* cf. *minimus*, late Pleistocene.

Locality and measurement	\bar{X}	OR	N
Clark's Cave, Va.			
p4 - m3, alveolar length	5.38	5.33-5.40	4
p4 - m3, occlusal length	4.85	4.75-4.95	4
Back Creek Cave No. 2, Va.			
P3 - M3, occlusal length	c. 5.33	-----	1

the Itasca Bison Kill Site in northcentral Minnesota (Shay, 1971).

Eutamias minimus is now known from one other Appalaehian cave site, a raptor-roost deposit of similar age, Back Creek Cave No. 2, Va., 24 km southwest of Clark's Cave (CM 29727, maxilla with P3-M2).

This strictly diurnal hibernating rodent would not be expected to bulk as large in the deposit as nocturnal small mammals active the year round. It is possible that this small, mouse-size ground squirrel may have been more common than its remains would indicate.

Marmota monax Linnaeus—Woodchuck

MATERIAL: CM 24527. 1 right 1 left mandible; skull fragments. MNI = 2 individuals.

REMARKS: A common species in late Pleistocene Appalachian cave deposits, this large terrestrial ground squirrel ranges throughout the deciduous and coniferous woodlands of east-central and northern North America north to Alaska and Labrador. Occlusal length p4-m3 is 18.9 mm.

Spermophilus tridecemlineatus (Mitchill)—
13-lined Ground Squirrel

MATERIAL: CM 24531. 5 left, 5 right whole or partial mandibles; 2 right maxillae. MNI = 5 individuals.

REMARKS: Remains of the 13-lined ground squirrel are generally distributed in eastern North American periglacial cave sites where they form from 4% to 10% (over 90% at Welsh Cave, Ky.) of the sciurids recovered. Remains are known from at least six other late Wisconsinan sites east of their present range: New Paris No. 4, Pa.; Bootlegger Sink, Pa.; Eagle Cave, W. Va.; Natural Chimneys, Va.; Welsh Cave, Ky.; Robinson Cave, Tenn. They have also been reported from Cumberland Cave, Md., late Kansan in age. The 13-lined ground squirrel was apparently common and widespread throughout the East during late glacial times, a distinct indicator of semi-prairie or parkland conditions.

Remains of this nominally midwestern ground squirrel occur with those of the eastern chipmunk and the least chipmunk at Clark's Cave. These three species of ground squirrels coexist today only in a relatively small area, stretching from northern Wisconsin north and west of the Great Lakes to southern Manitoba, from 1,200 km to 2,400 km northwest of Clark's Cave (Fig. 18). This area defines the present day boundary between eastern coniferous/deciduous forest and grassland (Cushing, 1965), the

Illinoian and Canadian Biotic Zone contact of Dice, 1943. In this area today the chipmunk, *Tamias striatus* (deciduous woodland preference), the least chipmunk, *Eutamias minimus* (coniferous woodland preference), and the 13-lined ground squirrel, *Spermophilus tridecemlineatus* prairie preference), find an intermesh of habitats enabling them to occur sympatrically, if not on identical ground, at least in such proximity that they can be harvested by raptors operating from a single roost, as at Clark's Cave.

Alveolar length of P3-M3 from one individual was 7.46 mm. Alveolar length of p4-m3 from eight examples was \bar{X} 7.76 mm (OR was 7.37-8.2).

Sciurus cf. carolinensis Gmelin—Gray Squirrel

MATERIAL: CM 29612. 1 left M2 (unerupted); 1 right M2 or M3 (extreme tooth wear); 1 M3 (slight tooth wear); 1 left, 1 right p4; 1 left, 1 right m1; 1 right m1 or m2; 1 left 1 right m3. MNI = 3 individuals.

REMARKS: The gray squirrel found primarily in deciduous mast-producing forest was probably not a member of the boreal fauna at Clark's Cave. It is common throughout the Appalachians north to New Brunswick. Farther north only the red squirrel, *Tamiasciurus hudsonicus*, occurs.

The persistence of the gray squirrel in western Virginia during full glacial times would have been governed by the type of forest cover. Pollen analysis at Hack and Quarles Pond in the Shenandoah Valley, at approximately the same altitude as both Natural Chimneys and Clark's Cave, seems to indicate that the western valley floor of the state supported a coniferous boreal forest within which one would not expect the gray squirrel to occur (Craig, 1969).

At the New Paris Pa., sinkholes, gray squirrel was the common tree squirrel recovered from the Recent Sinkhole No. 2 fauna. Only red squirrel remains were present in the boreal late Pleistocene Sinkhole No. 4 fauna.

One maxilla of gray squirrel was recovered from the late Pleistocene Natural Chimneys, Va., local fauna (CM 7536), in association with five red squirrels. The red squirrel is also the commonest squirrel in the Clark's Cave fauna (MNI 25).

The ten molars recovered were from at least three individuals, judging from the various states of toothwear. They agree in size with modern Pennsylvania comparative material and are not large enough to be those of fox squirrel, *Sciurus niger*.

Tamiasciurus hudsonicus (Erxleben)—Red Squirrel

MATERIAL: CM 24534. 13 left, 25 right whole or partial mandibles; 8 left, 4 right maxillae; 1 premaxilla. MNI = 25 individuals.

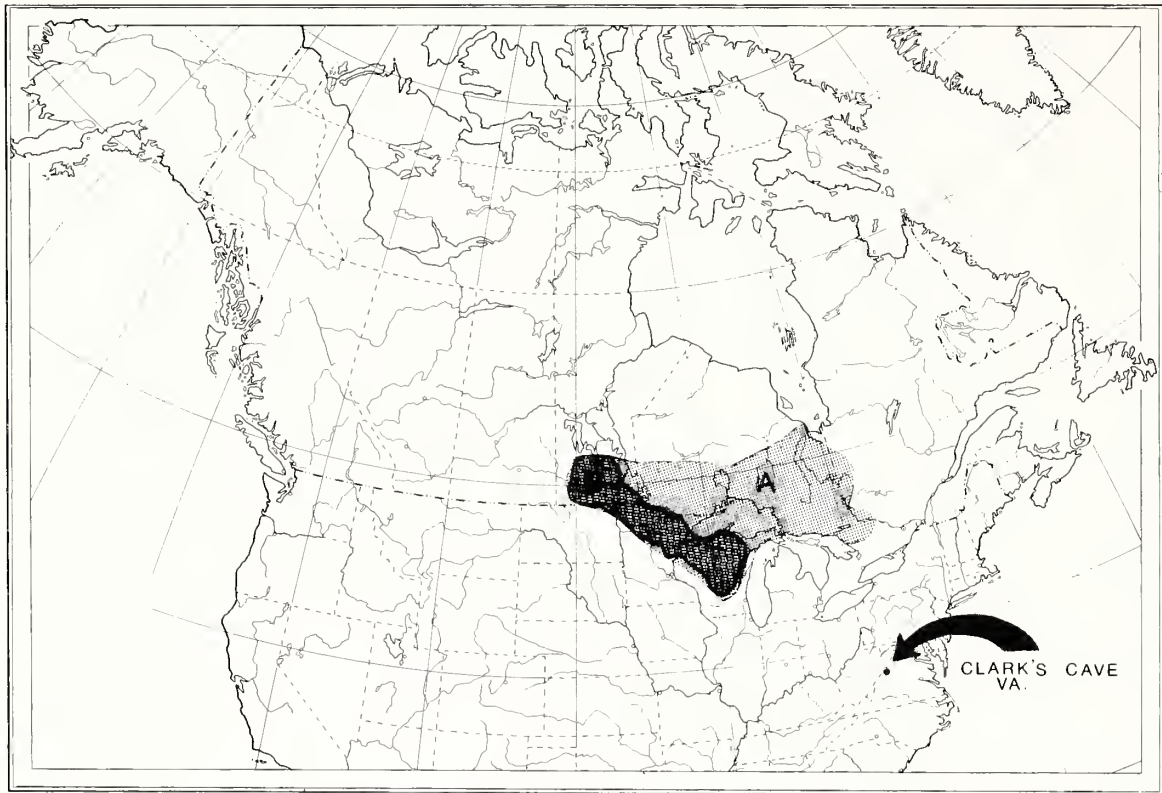


Fig. 18. Modern range overlaps of three species of terrestrial sciurids from Clark's Cave local fauna. A = overlap least chipmunk, *Eutamias minimus* (Bachman), and eastern chipmunk *Tamias striatus* (Linnaeus). B = overlap *E. minimus*, *T. striatus*, and 13-lined ground squirrel, *Spermophilus tridecemlineatus* (Mitchell).

REMARKS: The common large tree squirrel of Appalachian late Pleistocene sites, the red squirrel, accounted for 26% of the sciurids from the deposit. The red squirrel, the most widely distributed North American sciurid, ranges throughout the northern boreal forest from Alaska to Labrador, south in the Rocky Mountains to New Mexico in the West, in the Appalachian Mountains to North Carolina in the East. Commonest in coniferous forests, it is a very adaptable squirrel, and may occur in deciduous hardwood south to Iowa, Illinois, and North Carolina (Hall & Kelson, 1959). It occurs at the site today.

The Clark's Cave material is so fragmentary that the only measurements that could be taken were alveolar length of P4-M3 and p4-m3. P4-M3, one observation, was larger than that of thirty modern examples of *T. h. loquax* from Pennsylvania (Table 14). It was comparable in size to specimens from northwestern North America. Measurements of p4-m3 also indicate a large form, although this measurement is difficult to take with consistency, and is biased toward larger size by the sloping p4 and

erosion of the anterior alveolar wall. Alveolar length of p4-m3 may exceed occlusal length by as much as 0.5 mm, but even when this correction is made it is evident that the Clark's Cave *Tamiasciurus* material is of larger size than Recent eastern specimens, and is comparable to Recent Northwestern and late Pleistocene New Paris No. 4, Pa. material.

Genus *Glaucomys* Thomas—Flying Squirrels

Glaucomys sabrinus (Shaw)—

Northern Flying Squirrel

MATERIAL: CM 24529. 28 left, 22 right whole or partial mandibles; 8 left, 13 right maxillae. MNI = 28 individuals.

Glaucomys volans (Linnaeus)—

Southern Flying Squirrel

MATERIAL: CM 24530. 15 left, 19 right whole or partial mandibles; 1 left, 2 right maxillae. MNI = 19 individuals.

REMARKS: Flying squirrels comprised about 42% of the eight species of sciurids from the deposit, and 63% from Natural Chimneys, Va., high figures that clearly reflect the activity of nocturnal birds of

Table 14. Measurements (in mm) of *Tamiasciurus hudsonicus*.

Age and locality	\bar{X}	OR	SD	CV	N
P4 – M3, occlusal length					
<i>Recent:</i>					
Pennsylvania ¹	7.37	6.7–8.1	-----	-----	30
Natishquan R., Que., Hamilton R., Lab. ¹	7.58	7.2–8.4	-----	-----	17
Hudson Bay, Que. ¹	7.75	7.5–8.1	-----	-----	16
Moorhead, Minn. ¹	7.85	7.2–8.4	-----	-----	10
Aklavik, NWT, Seward, Alaska ¹	8.09	7.7–8.4	-----	-----	9
<i>Late Pleistocene:</i>					
Clark's Cave, Va.	8.4	-----	-----	-----	1
p4 – m3, occlusal length					
<i>Recent:</i>					
Pennsylvania ¹	7.39	6.8–7.8	-----	-----	33
Natishquan R., Que., Hamilton R., Lab.	7.66	7.3–8.0	-----	-----	20
Hudson Bay, Que. ¹	7.84	7.6–8.2	-----	-----	15
Moorhead, Minn. ¹	7.92	7.2–8.5	-----	-----	11
Aklavik, NWT, Seward, Alaska ¹	8.20	8.0–8.4	-----	-----	9
<i>Late Pleistocene:</i>					
New Paris No. 4, Pa. ¹	8.20	8.0–8.3	-----	-----	4
p4 – m3, alveolar length					
<i>Late Pleistocene:</i>					
Clark's Cave, Va.	8.68	8.15–9.2	.3	3.46	20

¹Measurements from Guilday *et al.*, 1964.

prey. Percentages for the diurnal chipmunk (*Tamias striatus*), 23% and 14% respectively, were much lower. In contrast with these figures, derived from raptorial bird roost-litter, remains of nocturnal flying squirrels from the pit-trap sinkhole at New Paris No. 4, Pa., comprised only 19% of all squirrels, and were greatly exceeded in numbers by diurnal terrestrial chipmunks (31%).

As at other late Pleistocene cave deposits from the central Appalachians, New Paris No. 4, Pa., and Natural Chimneys, Va., there were two species of *Glaucomys* present. The larger is identified as *G. sabrinus*, the smaller species as *G. volans*. They were sharply differentiated in size, with no overlap in observed ranges, and had a mean size-differential of 16% in alveolar length of p4-m3 (Table 15).

Late Pleistocene representatives of both species are larger than those now present in the central Appalachians. Samples of *G. volans* from New Paris No. 4, Pa., Natural Chimneys, Va., and Clark's Cave, Va., average 8% larger than modern Pennsylvania specimens, although there is an overlap in the ob-

served ranges (Table 15). Samples of *G. sabrinus* from the same cave deposits, however, average 14% larger than Recent *G. sabrinus* from the Appalachians in alveolar length of p4-m3 with no overlap in their respective observed ranges (Table 15). They do agree in size with specimens from the northern and western portions of the Recent range. Alveolar length of p4-m3 is a difficult measurement to take with accuracy because the anterior root of p4 slopes anteriorly away from the crown. In fossil specimens the anterior wall of the alveolus of p4 is often broken or eroded in varying degree. This would have the effect of lengthening the measurement. Despite this source of error, the size differential appears to be a real one. Both *G. volans* and *G. sabrinus* were larger during late Wisconsinan times in the Appalachians than are their modern counterparts, a reflection of cooler conditions, expressed as "Bergmann's Response."

Glaucomys volans occurs today throughout the state at all elevations and in all forest types (Handley & Patton, 1947). *Glaucomys sabrinus*, on the other

hand, has been taken in Virginia only at the highest elevations (Handley, pers. comm.). It occurs in the mountains directly west of Bath County, in West Virginia, at elevations exceeding 900 m. It has been taken as far south, in the Appalachians, as Tennessee and North Carolina at altitudes ranging from 1,200 m to 1,500 m (Handley, 1953). *Glaucomys volans* ranges north to approximately the United States/Canadian border in eastern North America, and south to the Gulf coast. *Glaucomys sabrinus*, on the other hand, ranges throughout forested Canada and south along both the Rocky Mountain and Appalachian Mountain chains at increasingly higher altitudes. *G. sabrinus* is primarily a squirrel of northern coniferous/hard-

wood forests and taiga, while *G. volans* is more characteristic of deciduous temperate forests. Both overlap in distribution in the northern Great Lakes area and the central Appalachians, and may be found in the same woodlots in some mountain areas. *G. volans* occurs commonly in the Clark's Cave area today. The presence of *G. sabrinus* in such large numbers at the site is certainly indicative of former boreal conditions. The presence of *G. volans*, however, does not necessarily indicate temperate conditions, as the fossil population is separable by size from its modern equivalent. This presumably has physiological implications.

Table 15. Measurements (in mm) of alveolar length lower toothrow (p4-m3) of *Glaucomys*.

Age and locality	\bar{X}	OR	SD	CV	N
<i>Glaucomys sabrinus</i> (Shaw) ^{1,2}					
<i>Late Pleistocene:</i>					
New Paris No. 4, Pa.	7.7	7.6-8.1	—	—	3
Natural Chimneys, Va.	7.8	7.3-8.4	—	—	14
Clark's Cave, Va.	8.0	7.6-8.6	.01	1.19	30
Robinson Cave, Tenn.	7.8	7.0-8.7	—	—	8
<i>Recent:</i>					
Eastern United States:					
<i>G. s. coloratus</i>	6.9	6.7-7.1	—	—	7
<i>G. s. fuscus</i>	6.7	6.5-6.9	—	—	5
<i>G. s. macrotus</i>	6.6	6.0-7.0	—	—	23
Canada:					
<i>G. s. sabrinus</i>	7.2	6.8-7.6	—	—	4
<i>G. s. makkovikensis</i>	7.1	6.9-7.4	—	—	2
Alaska:					
<i>G. s. zaphaeus</i>	7.6	7.3-7.9	—	—	5
Idaho:					
<i>G. s. bullatus</i> (=bangsi, Mayer, 1941)	8.7	8.6-8.7	—	—	7
<i>Glaucomys volans</i> (Linnaeus) ³					
<i>Late Pleistocene:</i>					
New Paris No. 4	6.4	—	—	—	2
Natural Chimneys, Va.	6.5	6.3-6.9	—	—	17
Clark's Cave, Va.	6.7	6.3-7.3	.18	2.67	17
Robinson Cave, Tenn., Armadillo Pit	6.3	6.2-6.6	—	—	5
Robinson Cave, Tenn., Sloth Pit	6.6	6.4-6.8	—	—	4
<i>Recent:</i>					
Pennsylvania ⁴	6.0	5.6-6.4	—	—	38

¹Measurements from Howell, 1918; Handley, 1953; Guilday *et al.*, 1964.

²Alveolar length of upper toothrow, when found in the literature, was converted to alveolar length of lower toothrow by multiplying by 0.94, a constant found to work out with modern Pennsylvania specimens.

³Data from Guilday, 1962; Guilday *et al.*, 1964, 1969.

⁴Unpublished measurements, J.K. Doult, CMNH Recent mammal collection.

Family: Cricetidae—Deer Mice and Woodrats

Genus *Peromyscus* Gloger

MATERIAL: CM 24682-28685, 29571. 221 left, 163 right mandibles; skull fragments and isolated teeth. MNI = 221 individuals.

Peromyscus maniculatus (Wagner)—Deer Mouse

MATERIAL: CM 29569. 41 ml's. An estimated minimum of 117 individuals based upon percentage of identified ml's of *P. maniculatus* and *P. leucopus*.

Peromyscus leucopus (Rafinesque)—
White-footed Mouse

MATERIAL: CM 29570. 37 ml's. An estimated minimum of 104 individuals based upon percentage of identified ml's of *P. maniculatus* and *P. leucopus*.

REMARKS: Remains of both *P. maniculatus* and *P. leucopus* were present in the collection in about equal numbers. Identifications were based upon dental characters. The first lower molar of *P. leucopus* is slightly larger (Table 16) than that of *P. maniculatus* with a greater incidence of accessory styles and lophs, a more massive bilaterally symmetrical anteroconid, and a deeper anterior anteroconid reentrant. Out of a series of 91 *Peromyscus* ml's selected at random, 14% could not be assigned to species either because of heavy toothwear or intermediate morphology. Of the remaining teeth,

41 (53%) were identified as *P. maniculatus*, 37 (47%) as *P. leucopus*.

Three nights of trapping by Dr. Charles O. Handley, Jr. and students of the University of Virginia in August, 1974, sampling talus, hilltop deciduous woods, woods-meadow ecotone, and hayfields surrounding the cave, produced 52 *P. leucopus* in 2000 trap nights. *Peromyscus maniculatus* apparently no longer occurs at or near the site.

Both species are common woodland forms in the state today. *P. leucopus* occurs everywhere except in the higher mountain summits. *P. maniculatus* is confined to cooler mountain forests above an elevation of 750 m (Handley & Patton, 1947).

It is possible that the percentage of *P. leucopus* to *P. maniculatus* increased in the cave area as the environment changed during the depositional history of the site, and that the 50/50 ratio of the identified material represents an average figure bridging a transition from predominantly *P. maniculatus* in late glacial times to 100% *P. leucopus* during the Holocene. Stratigraphic evidence from New Paris No. 4 suggests that this did occur in central Pennsylvania. In that fissure deposit, *P. maniculatus* formed 96% of the total *Peromyscus* recovered at the 8-10-m depth, but at the 0.25-m level was completely replaced by

Table 16. Measurements (in mm) *Peromyscus*, Clark's Cave. Late Pleistocene.

	\bar{X}	OR	SD	CV	N
Length m1 – m3					
<i>Peromyscus</i> , ?species CM 24682	3.4	3.1–3.7	.14	4.20	48
Length m1					
<i>P. cf. maniculatus</i> CM 29569	1.53	1.43–1.68	.05	3.26	41
<i>P. cf. leucopus</i> CM 29570	1.59	1.47–1.72	.06	3.86	37
above combined	1.56	1.43–1.72	.06	4.40	78
Width m1					
<i>P. cf. maniculatus</i> CM 29569	.81	.71–.98	—	—	41
<i>P. cf. leucopus</i> CM 29570	.85	.67–.96	—	—	35
$\frac{\text{Width m1} \times 100}{\text{Length m1}}$					
<i>P. cf. maniculatus</i> CM 29569	52.5%	45.8%–61.2%	—	—	40
<i>P. cf. leucopus</i> CM 29570	53.5%	44.3%–62.5%	—	—	36

P. leucopus, the only species presently living at the site.

No evidence of golden mouse, *Ochrotomys nuttalli* (Harlan), or harvest mouse, *Reithrodontomys humilis* (Audubon and Bachman), small rodents with a dental morphology somewhat similar to *Peromyscus*, was noted. Both occur sparingly in western Virginia today on the northern edges of their ranges (Handley & Patton, 1947; Wilder & Fisher, 1972).

Neotoma floridana (Ord)—Woodrat

MATERIAL: CM 24536. 10 left, 12 right mandibles with at least m1 in place; 25 left, 39 right isolated m1's; 22 left, 34 right mandibles with no dentition; 1 skull; 3 palates; 21 left, 18 right maxillae. MN1 = 51 individuals.

REMARKS: The woodrat is present at the site today. Five were trapped by C. O. Handley, Jr. and party in August, 1974. Woodrat droppings (15,000 estimated by weight) were the commonest organic items in the deposit, other than bones and teeth.

The woodrat is common in the southern and central Appalachians at all elevations, wherever suitable cliff/cave/talus habitat occurs. It does not range farther north than southern New York and western Connecticut (Hall & Kelson, 1959). Its failure to extend its range farther north in the Appalachians may be due to lack of suitable habitat rather than to climatic conditions *per se*. Other species of *Neotoma* occur in the mountains of western North America north to southern Alaska. Despite its modern temperate distribution, *Neotoma* was probably a member of the boreal late Pleistocene fauna at the

site. *Neotoma* remains in association with boreal small mammals are known from New Paris sink-hole No. 4, Pa. *N. f. magister*, the northeastern race, probably occupied most of its present range, south of the glacial terminal moraine, throughout the Wisconsinan glaciation at least.

Measurements of Clark's Cave woodrat dentitions do not differ significantly from those of modern Pennsylvania comparative material (Table 17).

In *Neotoma*, occlusal area increases with tooth wear. Therefore comparisons can only be made between specimens of comparable age. The dentitions were ranked in three relative age classes: (1) light — wear pattern established on occlusal surfaces, but not yet fully developed; (2) medium — wear pattern fully developed, but reentrants not isolated by cingular wear; (3) heavy — at least some reentrants isolated by cingular wear. Occlusal length of molars in the first wear class is significantly shorter. These were calculated separately. In a sample of 68 m1's from Clark's Cave, 51% showed light wear, 44% showed medium wear, and 5% heavy wear.

Family: Arvicolidae—Voles
(see Kretzoi, 1962)

Clethrionomys gapperi (Vigors)—Red-backed Vole

MATERIAL: CM 24519: 41 left, 27 right mandibles with m1; 3 left, 2 right m1's; 8 left, 7 right mandibles, no dentition; isolated upper molars. CM 24559: right m1 (Fig. 19K). CM 24560: right M3 (Fig. 19C). CM 24570: 84 left, 107 right mandibles with m1; 141 left, 168 right m1's; 154 left, 162 right M1's; 786 other molars. MN1 = 305 individuals.

Table 17. Dental measurements (in mm) *Neotoma floridana* (Ord).

Locality	Toothwear	\bar{X}	OR	N
Occlusal length m1 — m3				
Clark's Cave, Va.	Medium & heavy	9.8	9.3–10.2	5
Pennsylvania, Recent	Medium & heavy	9.7	9.5–10.2	15
Occlusal length m1				
Clark's Cave, Va.	light	3.4	3.1–3.9	34
Clark's Cave, Va.	Medium & heavy	3.9	3.6–4.3	32
Pennsylvania, Recent	Medium & heavy	3.8	3.6–4.1	17
Occlusal length m2				
Clark's Cave, Va.	Medium & heavy	3.2	3.0–3.4	14
Pennsylvania, Recent	Medium & heavy	3.3	3.1–3.6	17
Occlusal length m3				
Clark's Cave, Va.	Medium & heavy	2.3	2.1–2.4	11
Pennsylvania, Recent	Medium & heavy	2.3	2.1–2.5	15

Specimens examined: Recent, Pa.: CM Mammal No's. 29170, 73, 74, 76, 77, 78, 79, 88; 32602, 04; 33545; 35078, 79, 82, 86, 89, 90; 38638, 41; 39337.

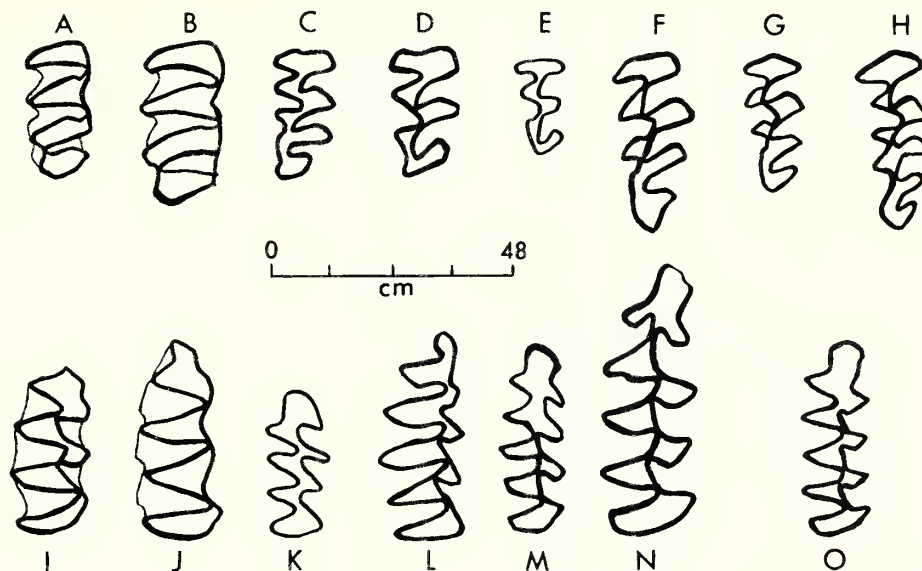


Fig. 19. Occlusal outlines of vole (Arvicolidae) molars, Clark's Cave local fauna, Bath County, Virginia. Cementum is indicated only for *Synaptomys*. UPPER ROW = right M3's: A. *Synaptomys cooperi*, CM 24566. B. *Synaptomys borealis*, CM 24564. C. *Clethrionomys gapperi*, CM 24560. D. *Phenacomys intermedius*, CM 24562. E. *Microtus pinetorum*, CM 24558. F. *Microtus xanthognathus*, CM 24553. G. *Microtus pennsylvanicus*, CM 24554. H. *Microtus chrotorrhinus*, CM 24555. LOWER ROW = right m1's: I. *Synaptomys cooperi*, CM 24565. J. *Synaptomys borealis*, CM 24563. K. *Clethrionomys gapperi*, CM 24559. L. *Phenacomys intermedius*, CM 24561. M. *Microtus pinetorum*, CM 24557. N. *Microtus xanthognathus*, CM 24552. O. *Microtus pennsylvanicus* or *chrotorrhinus*, CM 24556.

REMARKS: The red-backed vole is one of the commonest small mammals in the mountains of western Virginia. It is a forest vole of boreal affinity characteristic of northern coniferous forests of the Hudsonian and Canadian Life Zones and ranges south along the mountain summits of the Appalachians to northern Georgia. It does not occur at the site today despite the inviting appearance of the cool, shaded, cliff-based habitat. Extensive trapping in 1974 in and around the site failed to produce it. While it is common at higher elevations in the mountains, it is no longer present at the lower altitude of the Cowpasture River valley. Its presence in the deposit reflects former cooler woodland conditions near the site.

Red-backed voles accounted for 15% of the eight species of voles represented at Clark's Cave, 17% at Natural Chimneys, Va., and 21% at New Paris No. 4, Pa. No direct assessment of forest cover can be ascertained from such figures. At Sinkhole No. 4, Pa., within a vertical span of 4 m of continuous fissure fill, numbers of *Clethrionomys* increased from

4% at the lower level to 50% at the higher level. Correlated with this was a relative decline of field forms reflecting a period of floral change from open parkland to a closing coniferous forest. The vole assemblage, with the exception of *Dicrostonyx* at New Paris No. 4, is the same at all three sites—all dominated by *M. xanthognathus*. Unfortunately, the time span at Clark's Cave is not known, nor is any stratification apparent in the deposit itself, so that any internal changes in relative numbers of individual species could not be determined.

Clethrionomys remains were almost twice as common in the deposit as those of the woodland vole, *Microtus pinetorum* (MNI 305:170), the forest-inhabiting vole now present at the altitude of the site. This suggests that the boreal phase of the history of the site was the period of greatest depositional activity or duration. The sub-surface burrowing habits of *M. pinetorum* do not necessarily protect it differentially from predation. At a similar late Pleistocene owl roost, Natural Chimneys, Va., *M. pinetorum* was the more common of the two species

(MNI 47:65). *M. pinetorum* replaced the red-backed vole at lower altitudes in the central Appalachians as temperate conditions returned following the Wisconsin glacialiation. At New Paris, Pa., sinkholes No. 2 and No. 4 are located only a few meters apart. The *Clethrionomys*/*M. pinetorum* ratio changed from MNI 260:12 in the late Pleistocene boreal Sinkhole No. 4 fauna to MNI 0:51 in the Recent Sinkhole No. 2 assemblage.

In summary, *Clethrionomys* was a common species in the deposit, exceeded in MNI only by *M. xanthognathus*, *M. pennsylvanicus*, and *M. chrotorrhinus*, among the voles, and was almost twice as common as remains of *M. pinetorum*, the woodland vole now present at the site. This suggests that the boreal phase was the period of greatest depositional activity.

Phenacomys intermedius Merriam—Heather Vole

MATERIAL: CM 24515: 4 left, 5 right mandibles with m1; 1 left m1; 3 left, 1 right mandible, no dentition; 7 additional molars. CM 24561: right m1 (Fig. 19L). CM 24562: right M3 (Fig. 19D). CM 24571: 3 left mandibles with m1; 3 right mandibles with m1; 3 right mandibles, no dentition; 26 left, 12 right m1; 33 M1; 13 M2; 11 M3; 57 additional molars. MNI = 34.

REMARKS: This boreal rodent is no longer found in the eastern United States. It inhabits northern coniferous forest from the southern Yukon east to the Labrador coast. Unlike the northern bog lemming, *Synaptomys borealis*, which has a similar modern geographic distribution in eastern North America, *Phenacomys* does not occur south of the St. Lawrence estuary in the mountains of New Brunswick and northern New England.

Like the red-backed vole, *Clethrionomys*, the heather vole is not a grazer. Both genera, in contrast with all other American voles, have rooted molars, ill-suited for a diet of grasses. Heather vole remains at the site are, therefore, indicative of boreal forest of some type. Banfield (1974:193) summarizes its present habitat preferences, "Most have been taken in open, dry, coniferous forests of pine or spruce with an understory of heaths . . . usually near water . . . shrubby vegetation on the borders of forests and in moist, mossy meadows." It feeds on bark, buds, seeds and foliage of shrubs and forest understory.

Heather vole remains have been recovered from two other late Pleistocene cave sites in the state, Natural Chimneys and Back Creek No. 2. They were formerly widely distributed in late Pleistocene boreal faunas from periglacial eastern North America (Guilday & Parmalee, 1972).

Rarely taken by modern collectors, the heather vole is also rare in fossil collections: 3.6% of all voles at Natural Chimneys; 1.6% at Clark's Cave, and 3.8% at New Paris No. 4, Pa. It was the rarest vole in the Clark's Cave deposit.

Both boreal woodland forms, the relative abundance of *Phenacomys* and *Clethrionomys* remains in late Pleistocene sites from the central Appalachians are positively correlated: Clark's Cave, Va., 1.6% and 15%; Natural Chimneys, Va., 3.6% and 17%; New Paris No. 4, Pa., 3.8% and 21% of all voles respectively.

Microtus pennsylvanicus (Ord)—Meadow Vole

MATERIAL: CM 24521: 21 partial skulls plus maxillae and isolated molars for a total of 27 left M1, 31 right M1; 30 left M2; 26 right M2; 11 left M3, 7 right M3. CM 24554: right M3 (Fig. 19G). CM 24573: 138 left M1, 130 right M1; 262 left M2, 247 right M2; 294 left M3, 308 right M3. MNI = 316 individuals. Adjusted MNI = 658 individuals (69.3% of 950 *Microtus*, sp. m1's. See last paragraph of *M. chrotorrhinus* discussion for explanation of adjusted MNI).

REMARKS: The meadow vole is one of Virginia's commonest small mammals, occurring at all elevations in all meadow and grassy bog situations. The commonest species in the deposit, 24% of all terrestrial mammals, it is also the most widely distributed small vole in North America today. A closely related form, *M. agrestis*, the field vole, occurs widely in Europe and northern Asia as well. The two populations are now widely separated geographically but are obviously derived from a common stock (Klimkiewicz, 1970). Although the meadow vole occurred as far south as Florida during late Wisconsin times (Devil's Den, Martin, 1974b) it does not occur in the southeastern lowlands today. It ranges from South Carolina and the highlands of Georgia to northern Labrador, including all of Canada south of the tundra, west to the coast of Alaska. Modern barn owl pellets from the Clark's Cave cliffs yielded meadow vole remains, and they were trapped in the Cowpasture River valley by C. O. Handley, Jr., and party in 1974.

The abundance of *M. pennsylvanicus* remains in the deposit reflects not only the presence of suitable meadowlands in the river valley and the field-hunting predilections of the owls, but the fact that this was the only rodent in the deposit that was probably taken in undiminished numbers throughout its depositional history. It would have been the species least affected by the climatic change from the boreal late Pleistocene period to modern temperate in the central Appalachians. As long as moist grassy

areas were present, so was this vole.

Microtus pennsylvanicus was also the commonest species of terrestrial mammal recovered from both Natural Chimneys, Va., and New Paris No. 4, Pa. At only one site analyzed to date was it relatively uncommon: the Recent New Paris No. 2, Pa. (3 *M. pennsylvanicus*, 51 *M. pinetorum*). This is because animals trapped in New Paris No. 2 were only those whose immediate home ranges included the sinkhole entrance into which they tumbled. Had the deposit been an old owl roost accumulation like that at Clark's Cave, *Microtus pennsylvanicus* would have been present in large numbers concentrated by meadow-foraging owls. The dry woodland surrounding the mouth of New Paris No. 2 does not support *M. pennsylvanicus* even though it is regionally common.

Dentitions of this species from central Appalachian fossil deposits, as well as those of *M. xanthognathus* and *M. chrotorrhinus*, agree in having a lower first molar exhibiting a pattern of five closed triangles between the posterior crescent and the anterior trefoil (ml of *M. pinetorum* has three closed triangles, the fourth and fifth being broadly confluent). This advanced condition and their abundance in such sites makes them convenient horizon-markers. *Microtus* molars with five triangles are not present in earlier Pleistocene deposits, e.g., those at Cumberland Cave, Md. (late Kansan), and Trout Cave, W. Va. (Kansan/Yarmouthian). Instead, ml's of a simpler evolutionary grade, possessing three to four triangles, are present (van der Meulen, unpublished).

Microtus chrotorrhinus (Miller)—Rock Vole

MATERIAL: CM 24520: left maxilla with M1-M3; partial skull with left M1-M2, right M2-M3; 3 M3. CM 24555: right M3 (Fig. 19H). CM 24574: 3 left, 3 right M1; 3 left, 6 right M2; 102 left, 135 right M3. MN1 = 140 individuals. Adjusted MN1 = 292 individuals (30.7% of 950 *Microtus*, sp. m1, see last paragraph, this discussion).

REMARKS: The rock vole has never been trapped in Virginia but may possibly occur on some of the higher mountain summits. This animal has one of the most aberrant habitats of any North American *Microtus*. During the boreal episode of late Wisconsinan times the rock vole enjoyed a much wider geographical distribution in eastern North America. But following the retreat of the Wisconsinan ice sheet, its range in the central and southern Appalachians has been reduced to small disjunct populations in rocky areas of cool mountain forests above 900 m. Its continued presence in the southern and central Appalachians is due solely to the persistence of such

ecological enclaves, but it is absent in most of them now. Post-Wisconsinan range adjustment of *M. chrotorrhinus* consisted of local extinction and retreat to higher altitudes in the southern portions of its range, coupled with colonization of suitable northern areas as coniferous forest advanced into recently ice-freed areas. There were apparently few or no adaptive changes on the part of the animal itself. R. L. Martin (1973), in a detailed study of 464 Recent specimens from over 55 localities from Labrador to North Carolina, found no indication of clinal variation in the dentition. He did find a random pattern of variation from site to site caused by restricted gene flow between widely scattered populations marooned, as it were, on boreal "islands" in the eastern deciduous forests. The late Pleistocene sample of cranial material and dentitions from New Paris No. 4, Pa., is indistinguishable from *M. chrotorrhinus* in every character studied by Martin, but it averages somewhat larger in length of toothrow than modern central Appalachian material. Unfortunately, the *M. chrotorrhinus* sample from Clark's Cave was too fragmentary for measurement of other than isolated teeth.

The ratio of *M. chrotorrhinus* to *M. pennsylvanicus* varies from 4.8% at Natural Chimneys, Va., and 21.5% at New Paris No. 4, Pa., to a high of 30.7% at Clark's Cave. These varying percentages probably reflect the regional extent of rocky habitat favored by this species. The talus fronting the high Clark's Cave cliffs appears most favorable for this vole. Extensive trapping by C. O. Handley, Jr. and party in 1974, however, proves that *M. chrotorrhinus* no longer occurs at the site, despite the presence of cool, damp, forested, rocky tumbles. During a cooler episode, however, it would have made ideal habitat, providing a ready supply of rock voles for predators.

The identification and assessment of minimum numbers of individuals of all voles from the deposit, with the exception of *M. chrotorrhinus* and *M. pennsylvanicus*, was based upon counts of ml's. The largest and most readily identifiable tooth in vole dentitions, the ml has a greater percentage of recovery in the field, because of its larger size, than do the other relatively smaller molars. Unfortunately the ml's of *M. chrotorrhinus* and *M. pennsylvanicus* look alike, and minimum numbers of individuals of these two species had to be based upon the smaller but distinctive M3's. The combined total of these two species, based upon the more easily lost M3's was 456. However, a census of all *Microtus* ml's that could be referred to either species came to a mini-

imum of 950 individual animals, indicating a considerable loss in recovery of the smaller M3's. If this were the case, then minimum numbers of *M. chrotorrhinus* and *M. pennsylvanicus* could not be legitimately compared to minimum numbers of the other species of voles from the site. To remedy this, an adjusted minimum number of individuals for these two species was obtained by dividing the 950 MNI, based on m1's, by the relative percentages of *M. chrotorrhinus* to *M. pennsylvanicus* as indicated by M3 counts. This was also done at New Paris No. 4, Pa. (*M. pennsylvanicus* = 361, or 78.5% of *Microtus* sp.; *M. chrotorrhinus* = 99, or 21.5% of *Microtus* sp.), and Natural Chimneys, Va. (*M. pennsylvanicus* = 121, or 95.2% of *Microtus* sp.; *M. chrotorrhinus* = 6, or 4.8% of *Microtus* sp.). Some isolated M3's are of intermediate morphology and perhaps 5% were misidentified. But the chances of misidentification are reciprocal and this source of error probably does not influence the relative ratios of *M. chrotorrhinus* to *M. pennsylvanicus* based upon M3's from the site.

Microtus xanthognathus (Leach)—
Yellow-cheeked Vole

MATERIAL: CM 24522: 156 left, 194 right mandibles with m1; 21 left m1, 14 right m1; 5 left m3, 16 right m3; 79 partial skulls, 7 maxillae with 42 left M1, 42 right M1, 18 left M2, 25 right M2, 8 left M3, 10 right M3. CM 24552: 1 right m1 (Fig. 19N). CM 24553: 1 right M3 (Fig. 19F). CM 24572: 33 left, 42 right mandibles with m1; 288 left m1, 260 right m1, 110 left M1, 97 right M1, 31 left M2, 42 right M2, 182 left M3, 205 right M3; 4 partial skulls. MNI = 511 individuals.

REMARKS: The largest species of North American *Microtus* with an average weight three times that of *M. pennsylvanicus*, the yellow-cheeked vole was the single most important food item in the deposit. It was exceeded in numbers of individuals only by the meadow vole. Both species outnumbered all other terrestrial small mammals.

Despite its abundance, no other mammal in the deposit has adjusted its range so dramatically from that day to this. Remains of this vole have been recovered south of the late Wisconsinan ice moraines from late Pleistocene sites in Missouri, Iowa, Illinois, Kentucky, Pennsylvania, West Virginia, Virginia, and Tennessee. Its range has now shifted north almost 20° in latitude, some 1,900 km, to the taiga of western Canada and Alaska, where it is now rare, local, and seldom collected.

The yellow-cheeked vole was also a dominant small mammal at New Paris No. 4, Pa. (344 MNI). As at Clark's Cave, it was slightly exceeded in num-

bers by *M. pennsylvanicus* (361 est. MNI). When large numbers of *M. xanthognathus* were encountered at New Paris No. 4, Pa., there was some question about whether this species, so rare and local today, was present in such relatively large numbers regionally, or whether ecological conditions immediately surrounding the sinkhole mouth produced a local condition favorable to *M. xanthognathus*, creating a "hot spot" which did not reflect the regional picture. Its abundance at Clark's Cave, however, clarifies its regional significance. Instead of tumbling into a sink trap, the Clark's Cave *M. xanthognathus* were concentrated from a much larger area. They must have been abundant in the cruising range of the Clark's Cave raptors, sustaining their numbers over a long period of time, to bulk so large in the deposit.

Despite the different accumulation mechanisms at New Paris No. 4, Pa., and Clark's Cave, Va., and the fact that they are 240 km apart, both sites are located just east of the Appalachian Plateau in the now relatively dry intermontane valleys of the Ridge and Valley section of the Appalachians. Dry shale barrens are characteristic of both areas today, and the general character of the two sites, allowing for the difference in latitude, may have been similar during late Pleistocene times. The only other Virginia localities for fossil *M. xanthognathus*, Natural Chimneys and Back Creek No. 2, are also in the mountainous western portion of the state. This is probably a reflection of differential distribution of suitable fossil traps. Remains from Bootlegger Sink, Pa. (*M. xanthognathus*), and Little Kettle Creek, Ga. (*Clethrionomys*, *Synaptomys*, Voorhies, 1974), indicate that boreal small mammals were widely distributed in the eastern Piedmont south and east of their present ranges. The former widespread occurrence of *M. xanthognathus* in the American Midlands (Hallberg, Semken, and Davis, 1974) and its relative abundance in such sites strongly suggests that this now-rare vole was both widespread and common in eastern North America south of the continental Wisconsinan glaciation—a convenient index fossil for deposits of this age. It appears, however, not to have been present in western North America during this time. It has not been reported from numerous sites of comparable age in the central Rockies (Jaguar Cave, Ida.; Wilson Butte, Ida.; Little Box Elder Cave, Wyo.). Even today the animal is not found in mountainous terrain. It has not been reported from sites older than Wisconsinan. It was not present in the Appalachians in Kansan/Yar-

mouthian times (Cumberland Cave, Md.; Trout Cave, W. Va.) and the pre-Wisconsinan history of this species is unknown.

Unfortunately, this vole is so seldom collected and occurs so sporadically throughout its range, that habitat information of the living animal is sketchy and general. It occurs, randomly and unpredictably, in a variety of boreal woodland situations. Its range is included in the Hudsonian Biotic Province of Dice (Dice, 1943), the taiga, avoiding both barren-ground habitat to the north and the closed coniferous forests of the Canadian Biotic Province of southern Canada. In the taiga, however, it has been found in both moist valley sites and upland well-drained woodlands. It burrows extensively, appears to prefer friable soils, although it may occur in wet sphagnum bogs. It does not occur in grasslands, like *M. pennsylvanicus*, or in rocky wooded talus as does *M. chrotorrhinus*. All accounts of present habitat (Preble, 1908; Lensink, 1954; Banfield, 1974; Youngman, 1975) mention some form of woodland cover—a thin

boreal forest dominated by spruce and jackpine with a ground covering of heaths and sphagnum would accommodate this vole.

Although *M. xanthognathus* and *M. chrotorrhinus* are both boreal forest forms, with sympatric ranges in the mid-Appalachians during at least Wisconsinan times, their ranges are widely separated today. *M. xanthognathus* occurs in the western sub-Arctic, its known range separated from that of *M. chrotorrhinus* by approximately 800 km. *M. chrotorrhinus* is found only in the eastern sub-Arctic and as a relict form south in the higher Appalachians. Why have these two species gone their separate ways (Fig. 20)?

The following sketch agrees with the paleontological and geological facts, as far as they are known, and may explain the present distribution of these two species. Both species have been recovered from seven late Pleistocene sites (New Paris No. 4, Pa.; Bootlegger Sink, Pa.; Eagle Rock, W. Va.; Back Creek No. 2, Va.; Natural Chimneys, Va.; Clark's

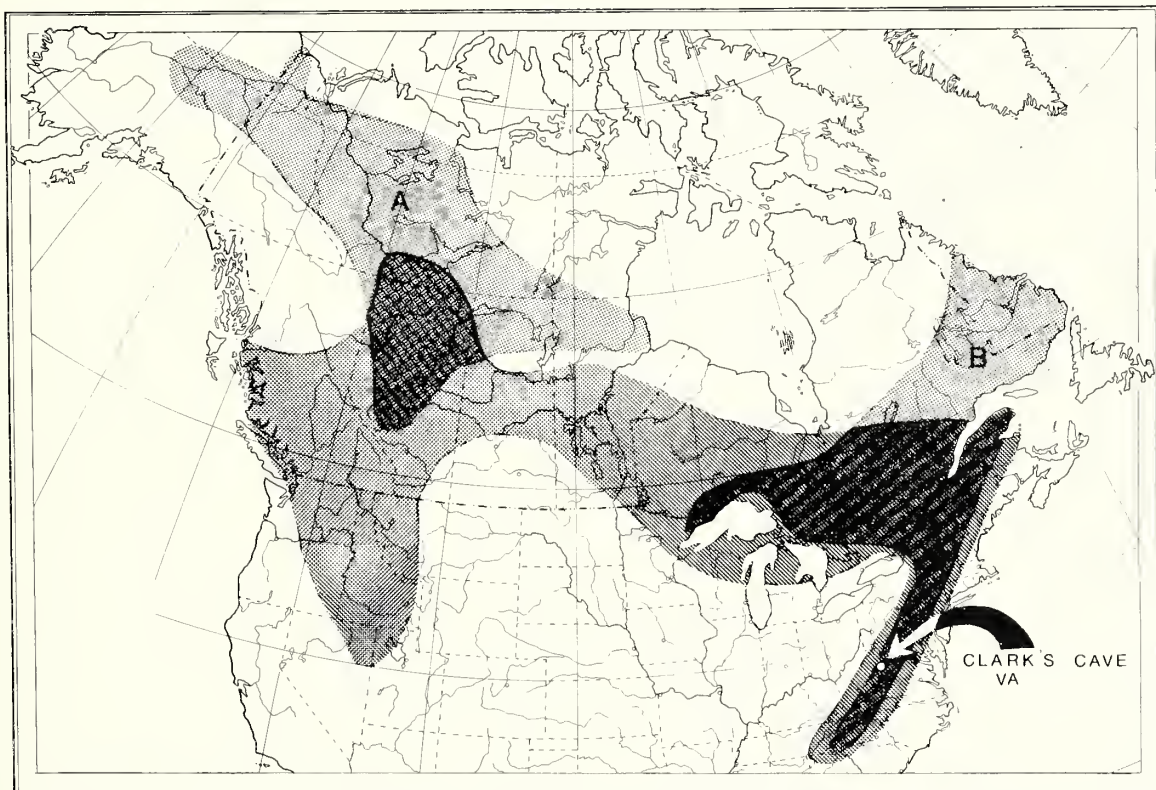


Fig. 20. Modern ranges of (A) Yellow-cheeked vole, *Microtus xanthognathus* (Leach); (B) Rock vole, *Microtus chrotorrhinus* (Miller); superimposed upon Canadian Life Zone; from Hall & Kelson, 1959. Appalachian portion of Life Zone highly generalized from true fragmented situation.

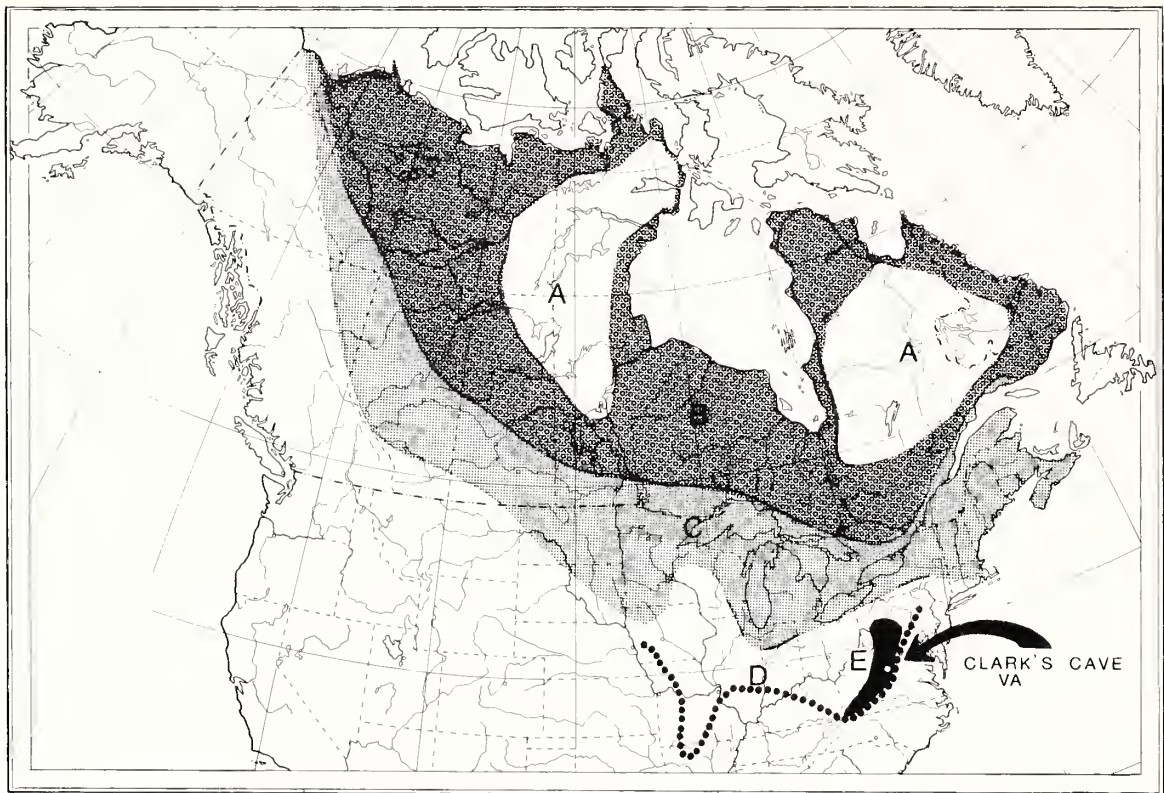


Fig. 21. Successive stages of continental Wisconsin glacial recession in central and eastern North America (from Bryson *et al.*, 1969), and periglacial ranges of yellow-cheeked vole, *Microtus xanthognathus* (Leach), (from Hallberg *et al.*, 1974) and rock vole, *Microtus chrotorrhinus* (Miller). A = ice cover, 7,000 years B.P. B = ice cover, 9,000 years B.P. C = ice cover, 12,000 - 13,000 years B.P. D = Wisconsin periglacial range of *Microtus xanthognathus* (Leach). E = Wisconsin periglacial range overlap, *M. xanthognathus*, *M. chrotorrhinus*.

Cave, Va.; and Baker Bluff, Tenn.) but all these sites are in or near the Appalachian Mountains. Sites farther west (Welsh Cave, Ky.; Meyer Cave, Ill.; Waubonsie local fauna, Iowa; Bat Cave, Mo.; Peccary Cave, Ark.) have produced remains of *M. xanthognathus* only (Fig. 21).

As post-glacial warming set in and the open boreal forest of periglacial central and eastern North America gave way to denser tree cover and more temperate conditions, *M. chrotorrhinus* was able to survive in the Appalachians by retreating to higher elevations. Its range fragmented in the central and southern Appalachians as suitable rocky boreal habitat became increasingly restricted. Density of tree cover apparently had little effect as long as the animal could resort to its preferred habitat. *M. xanthognathus*, however, became extinct in the Appalachians, as post-glacial reforestation produced a closed-canopy forest.

Continental meltback of the Wisconsin ice front proceeded much more rapidly in the American

Midlands than it did in the East (Fig. 21). Continental ice masses persisted in both Ungava and eastern Keewatin for thousands of years after an ice-free corridor in the Central Plains opened east of the Rocky Mountains north to Alaska. As this corridor opened to the Northwest, it was colonized by *M. xanthognathus* from the south. The animal's range shifted to the north *in toto*, advancing on its northern front, becoming extinct in its southern fringes as reforestation eclipsed its preferred habitat in that area. Unable to spread northeast into the eastern Arctic at this time because of the persistent ice block, or to continue in relict habitats in the Appalachians, as did *M. chrotorrhinus*, it could only follow the fortunes of the taiga as it retreated (or advanced?) to higher latitudes in the Northwest. When the eastern ice block melted, sometime after 7,000 years B.P. (Bryson *et al.*, 1969), eastern Keewatin, south of the barren ground, was duly colonized by *M. xanthognathus*. Access farther east to Ungava was blocked by Hudson Bay and by closed boreal

forests to the south. By the time Ungava was open to biotic invasion from the south, *M. xanthognathus* was extinct in the Appalachians. Hudson Bay has also acted as a barrier to the eastern post-glacial spread of the lemming *Dicrostonyx torquatus*, allowing the isolated *D. hudsonius* to survive in the tundra of Ungava (Guilday, 1963).

Microtus pinetorum (LeConte)—Woodland Vole

MATERIAL: CM 24524: 3 left, 4 right mandibles with m1; 7 left, 5 right m1. CM 24557: 1 right m1 (Fig. 19M). CM 24558: 1 right M3 (Fig. 19E). CM 24576: 24 left, 18 right mandibles with m1; 136 left, 114 right m1; 31 left, 33 right M3. MNI = 170 individuals.

REMARKS: The woodland vole, 8% of all voles in the deposit, was the least common of the four identified species of *Microtus* (Table 4). Although only *M. pennsylvanicus* was trapped in the area by C. O. Handley, Jr. and party in 1974, and present in a few barn owl pellets from the cliffs, *M. pinetorum* is undoubtedly present in the Cowpasture River valley wherever conditions are suitable for this semi-burrower. It is present throughout western Virginia at medium-to-low altitudes, in loose, friable soils of open woodlands, orchards, and field borders.

Identification to species is based upon geographic probability. It is conceivable that *M. ochrogaster* may be represented as well.

The woodland vole does not occur in the northern coniferous forests, reaching its northern limits at approximately the U.S./Canadian border. It is present in all late Pleistocene sites examined to date from the mid-Appalachians, and probably was present during the boreal episode of deposition.

It is replaced at higher elevations in the Appalachians today by the red-backed vole, *Clethrionomys gapperi*, another woodland form. At New Paris No. 4, Pa. (11,300 years B.P.), 260 *Clethrionomys*, but only 12 *M. pinetorum* (4.4% of their combined number) were recovered. At Clark's Cave, ratio of *M. pinetorum* to *C. gapperi* is 36%. This large relative increase at Clark's Cave may be due either to the presence of *M. pinetorum* in larger numbers during the boreal episode, or to deposition at Clark's Cave continuing on into more temperate times. We suspect the former. The occurrence of macrofossils of deciduous trees and shrubs (*Quercus*, *Corylus*) in a predominantly boreal spruce (*Picea*) flora and the apparent association of *Phenacomys*, *Clethrionomys*, *M. pennsylvanicus*, and *M. pinetorum* in alluvial silts of the Brayton local fauna of southwestern Iowa (Dulian, MS), dated at 12,420 ± 180 years B.P., a time near the final retreat of the Wisconsin ice

from Iowa, suggests that *M. pinetorum* may also have been at Clark's Cave during the boreal episode of deposition.

Ondatra zibethicus (Linnaeus)—Muskrat

MATERIAL: CM 24526. Partial palate with left m1-m2; 4 left, 3 right mandibles with m1; 2 right mandibles, no dentition. MNI = 5 individuals.

REMARKS: This is an abundant semi-aquatic species present at the site today and throughout most of temperate and boreal North America south of the tundra. The low number of muskrats from this riverbank site can be accounted for by their relatively large size and aquatic habits, protecting them from owl predation.

Synaptomys cooperi Baird—Southern Bog Lemming

MATERIAL: CM 24517: 1 right mandible with m1; 1 right mandible, no dentition; 1 left m1; 1 right m3. CM 24565: 1 right m1 (Fig. 19I). CM 24566: 1 right M3 (Fig. 19A). CM 24567: 2 right mandibles with m1; 22 left m1's, 18 right m1's. MNI = 23 individuals.

REMARKS: The southern bog lemming is relatively widespread in meadows, dry fields, and occasional bogs in western Virginia, at all altitudes (Handley & Patton, 1947:169). It is the rarest vole in the area. In the Appalachian Mountain region its range extends from the Great Smoky Mountains in the south, north through New Brunswick to southern Labrador. In the northern portions of its range *S. cooperi* is narrowly sympatric with the southern fringe of the range of the northern bog lemming, *S. borealis*. Although *S. cooperi* is more temperate in distribution, the ecological differences between the two species in their area of sympatry are not clear.

Both species were recovered from New Paris No. 4, Pa., where a stratigraphic shift in relative numbers made it apparent that *S. cooperi* gradually replaced *S. borealis* in the central Appalachians somewhere near 11,000 years B.P. as the climate ameliorated. *S. cooperi* accounted for 20% of all *Synaptomys* recovered at New Paris No. 4, Pa. At Clark's Cave the proportion of *S. cooperi* was somewhat greater, 27% of all *Synaptomys* (N = 84). This may reflect either a difference in the relative ages of the sites, an ecological difference caused by differing physical parameters, or a reflection of a longer period of deposition at Clark's Cave, extending into temperate times.

The *S. cooperi* remains from Clark's Cave agree in size with those from other late Pleistocene deposits in the central Appalachians (Table 18), smaller than the population now in the area. This probably

reflects a cold-stressed environment and it mirrors the present size cline of modern *S. cooperi*, i.e., an inverse size/latitude correlation. This, together with a relatively low coefficient of variation, suggesting a common gene pool, indicates that the *S. cooperi* remains at Clark's Cave were largely laid down prior to the advent of full-temperate conditions at the site.

Synaptomys borealis (Richardson)—
Northern Bog Lemming

MATERIAL: CM 24516: 7 left, 4 right mandibles with m1; 3 left, 5 right m1; 1 right m2; 1 left, 1 right m3. CM 24563: 1 right m1 (Fig. 19J). CM 24564: 1 right M3 (Fig. 19B). CM 24568: 4 left, 8 right mandibles with m1; 40 left, 43 right m1; 1 left, 1 right M1. MNI = 61 individuals.

REMARKS: This forest lemming is no longer found in the central or southern Appalachians. Its present range includes the boreal forest and taiga from Alaska to Labrador, south to Minnesota and the White Mountains of New Hampshire, 1,000 km northeast of Clark's Cave. Its habitat is variously described (Soper, 1942, 1948; Banfield, 1974) as ranging from moist to dry situations—grassy, second-growth spruce and poplar; thick gloomy spruce woods carpeted with sphagnum; grass-clumped willow swamp; small meadows; moist spruce woods; spruce bogs; alpine meadows.

Uncommon to rare throughout its range today, the northern bog lemming is commonly found in late Pleistocene deposits from the central Appalachians (New Paris No. 4, Pa.; Bootlegger Sink, Pa.; Eagle Cave, W. Va.; Bowden Cave, W. Va.; Natural Chimneys, Va.; Back Creek Cave No. 2, Va.; Guy Wilson Cave, Tenn.; Baker Bluff Cave, Tenn.; Robinson Cave Tenn.). Its remains are never present in large numbers, however. At New Paris No. 4 (MNI 71) it comprised only 5.8% of all voles recovered, at Clark's Cave (MNI 61) only 3% of all voles.

Occlusal length of 33 m1 from Clark's Cave, Va., averaged 2.88 mm, OR 2.5–3.2 mm, SD .04, CV 1.39. Eighty m1 from New Paris No. 4, Pa., averaged 2.91 mm, OR 2.3–3.2, SD .17, CV 5.84.

Family: Zapodidae—Jumping Mice

Zapus hudsonius (Zimmerman)—
Meadow Jumping Mouse

MATERIAL: CM 29572: 29 mandibles, with at least m1; 12 additional m1; 12 m2; 28 maxillae. MNI = 22 individuals.

REMARKS: The meadow jumping mouse is broadly distributed throughout northern North America, south of permafrost, from southern Alaska east to Labrador, south to Oklahoma, Alabama, and Georgia (Hall & Kelson, 1959:772). It prefers meadow and old-field situations of dense low vegetation, stream banks, and clearings in either open or forested country. *Zapus* is present at the site today; one was trapped in the hay fields above the cave in August, 1974, by C. O. Handley, Jr. It is present throughout the state wherever there is suitable habitat (Handley & Patton, 1947:182). Measurements of 36 lower first molars are: Total length, M = 1.5 mm; OR = 1.38 mm—1.70 mm. Measurements of 22 M2's are: Total length, M = 1.39 mm; OR = 1.26—1.57 mm.

Napaeozapus insignis (Miller)—
Woodland Jumping Mouse

MATERIAL: CM 29573: 15 mandibles with m1; 13 additional m1; 17 m2; 13 maxillae. MNI = 15 individuals.

REMARKS: The woodland jumping mouse does not occur at Clark's Cave today. It is closely confined to stream banks and woodland edge situations in the spruce/fir and hemlock/northern hardwood forests of eastern North America, from the Lake Superior region east to southern Labrador, thence south along the Appalachian Mountains at increasing altitudes to northern Georgia (Wrigley, 1972). In Virginia it is confined to mountain summit forests of cool, moist, rocky aspect in the western part of the state at higher elevations (Handley & Patton, 1947). *Napaeozapus insignis* exhibits a pronounced "Bergmann's Response." Individuals from the extreme southern portions of its range average some 12% smaller than those of eastern Canada (Wrigley, 1972). Specimens from the Clark's Cave deposit have greater dental dimensions than modern mid-

Table 18. Measurements (in mm) *Synaptomys cooperi* Baird, occlusal length m1.

Locality	\bar{X}	OR	SD	CV	N
Pennsylvania, Recent ¹	2.48	2.1–2.7	0.19	7.66	25
New Paris No. 4, Pa., late Pleistocene ¹	2.41	2.3–2.5	0.09	3.73	20
Clark's Cave, Va., late Pleistocene	2.40	2.2–2.7	0.11	4.75	33
Natural Chimneys, Va., late Pleistocene ¹	2.39	2.2–2.5	0.05	2.92	14

¹Data from Guilday, *et al.*, 1964: 162.

Table 19. Dental measurements (in mm) *Napaeozapus insignis* (Miller).

Age and locality	\bar{X}	OR	N
Total length m1			
Recent:			
Pennsylvania ¹	1.6	1.5–1.8	20
Late Pleistocene:			
New Paris No. 4, Pa. ¹	1.8	1.7–2.1	11
Natural Chimneys, Va. ¹	1.7	1.6–1.7	6
Clark's Cave, Va.	1.7	1.6–1.9	27
Total length m2			
Late Pleistocene:			
Clark's Cave, Va.	1.6	1.5–1.8	21

¹Measurements from Guilday *et al.*, 1964: 168.

Appalachian material by some 7%. They compare most closely with late Pleistocene specimens from New Paris No. 4, Pa., and Natural Chimneys, Va. All three sites agree in the boreal nature of their respective faunas. The *Napaeozapus* from all three sites represent a late Pleistocene population in the mid-Appalachians, larger than the population now present in the area.

Family: Erethizontidae—Porcupines

Erethizon dorsatum (Linnaeus)—Porcupine

MATERIAL: CM 24528: 1 left mandible with full dentition; 2 upper molars. MNI = 1 individual.

REMARKS: There are no modern records for the porcupine in Virginia. It reaches its present southern limits as a breeding population in northern Pennsylvania (Doutt *et al.*, 1973). Porcupine remains have been recovered from Natural Chimneys, Va. It was apparently more widespread in karst areas immediately west of the Appalachians where it has been reported from Late Prehistoric archaeological sites as far south as Tennessee and Alabama (Parmalee & Guilday, 1966; Barkalow, 1961; Weigel, 1974). Primarily a denizen of coniferous, or northern hardwood, forests, the porcupine is also strongly attracted to rocky terrain and caves.

Family: Canidae

Canis, cf. *C. dirus* Leidy—Dire Wolf

MATERIAL: CM 29611: 1 right unciform. MNI = 1 individual.

REMARKS: Large mammal remains are rare in the deposit. The single carpal is 20% larger than a comparable unciform of a large male timber wolf, *C. lupus* from Alaska (CM mammal no. DC 1247). It is referred with confidence to the dire wolf because

of its size and the late Pleistocene age of the bulk of the collection.

The dire wolf is the only species of wolf present in Appalachian deposits of Wisconsinan age. It was replaced by the timber wolf following its extinction at the close of the Pleistocene.

Direct comparison was made with the Clark's Cave unciform and the adjacent carpal, an os magnum, of the Powder Mill Creek Cave, Mo., *C. dirus* skeleton (Catalog No. P-249, Galbreath, 1964). They were of comparable size.

Measurements of CM 29611 are: greatest depth, 22.2 mm; length metatarsal IV facet, 17.4 mm, approx.; width metatarsal IV facet, 17.1+ mm. (*C. lupus* DC 1247 = 17.5 mm, 13.1 mm, 15.0 mm, respectively).

Family: Ursidae

Ursus americanus Pallas—Black Bear

MATERIAL: CM 24592: 1 m2. CM 29696: 1 phalanx. MNI = 1 individual.

REMARKS: Definitely not a raptor prey item, the isolated tooth and phalanx were probably deposited by hoarding woodrats. Measurements of the m2 are: length of crown, 15.5 mm; width of crown, 10.7 mm. This agrees well with measurements of 17 sixteenth-through-seventeenth-century archaeological specimens from two late prehistoric sites in West Virginia (46 Pu 31 and 46 Fa 7): length 15.3 mm (13.1–17.7 mm), width 11.8 mm (10.7–13.3 mm). The black bear is still found in the mid-Appalachians.

Family: Procyonidae

Procyon lotor (Linnaeus)—Raccoon

MATERIAL: CM 24593: 1 right upper deciduous molar. MNI = 1 individual.

REMARKS: Adults are too large for the majority of raptors. The juvenile represented by this single molar may have been owl prey.

Family: Mustelidae

Martes americana (Turton)—Pine Marten

MATERIAL: CM 24954: distal half right humerus; distal half right tibia. MNI = 1 individual.

REMARKS: There is no evidence that the pine marten was ever found in Virginia during historic times. It did occur as far south as Pennsylvania in northern coniferous/hardwood forests (Rhoads, 1903). Paradiso, 1969, believes it to have been exterminated in the mountains of Maryland, "as far back as 85 years ago," and it once may have occurred in the ridgetop spruce forests of West Virginia. It is a common late Pleistocene cave fossil from the mid-Appalachians and has been reported from Eagle Cave, W. Va., Benedict's Cave, W. Va. (CM 24698), New Paris No. 4, Pa., Natural Chimneys, Va., and as far south as Robinson Cave in central Tennessee.

Genus *Mustela* Linnaeus

Mustela erminea Linnaeus—Ermine

MATERIAL: CM 24597: 1 left, 2 right maxillae with P4; 1 left, 2 right P4; 3 left, 2 right mandibles with m1; 1 right mandible, no dentition; left humerus, left femur, left tibia. MNI = 4 individuals.

Mustela nivalis Linnaeus—Least Weasel

MATERIAL: CM 24596: 6 left, 2 right P4; partial skull with P4; 3 left, 2 right mandibles with m1; 1 left, 1 right m1; 1 humerus. MNI = 7 individuals.

Mustela ?species, cf. *M. frenata* (female) or *M. erminea* (male)

MATERIAL: 29699: anterior half of skull with left P4-M1, right P2, right P4-M1. MNI = 1 individual.

Mustela vison Peale & Palisot de Beauvois—Mink

MATERIAL: CM 24595: partial skull; left mandible fragment; right humerus; 2 right femora; right tibia. MNI = 2 individuals.

REMARKS: The relative scarcity of carnivores in the deposit reflects the collecting bias of the birds of prey. Large species were either not represented at all, or by isolated teeth of fortuitous occurrence. A few small carnivores did find their way into the deposit as prey items, their numbers in inverse proportion to their size. The two weasels definitely present in the deposit, *M. erminea* and *M. nivalis*, are the two smallest North American carnivores.

The least weasel is rare in the state today but is probably present throughout the mountain counties

of the state (Handley & Patton, 1947). It is a circum-boreal species whose range extends along the Appalachian Mountains south to the Great Smokies. *M. erminea* has not been recorded, either living or fossil, as far south as Virginia. It, too, is a circum-boreal species, but reaches its present southern limits in northern Pennsylvania, where it is uncommon. There is one anomalous record from the Piedmont of Maryland (Vazquez, 1956).

Late Pleistocene remains of least weasel have been recovered from New Paris No. 4, Pa., Natural Chimneys, Va., and Back Creek No. 2, Va., in the central Appalachians, and west of the Appalachians, from Meyer Cave, Ill., Welsh Cave, Ky., and Robinson Cave, Tenn. *M. erminea*, however, has not previously been reported from the Pleistocene of eastern periglacial North America. It was present in the Conard Fissure, Ark., far south of its modern range (Brown, 1908).

M. frenata, the long-tailed weasel, the commonest species in Virginia today, is not definitely represented in the deposit. The possible partial skull listed above is not complete enough for identification. At least three *M. frenata* specimens were recovered from Natural Chimneys, Va., and the species was undoubtedly present in the Clark's Cave area at some period during the accumulation of the deposit.

Although the presence of *M. erminea* points to more boreal conditions in the area at one time, all weasels and mink occur in such a variety of ecological conditions throughout their range that they provide no definite paleoecological clues.

cf. *Mephitis mephitis* (Schreber)—Striped Skunk

MATERIAL: CM 24598: 1 ulna; 1 left, 1 right lower canine. 1 basicranial fragment.

REMARKS: The elements are too large for spotted skunk, *Spilogale*, and the identification is tentative because of the fragmentary nature of the specimens. The presence of the hooded skunk, *M. macroura*, or the hog-nosed skunk, *Conepatus* (Ladds Quarry, Ga.), in such a boreal deposit seems remote.

Family: Cervidae—Deer

cf. *Cervus elaphus* Erxleben—Elk

MATERIAL: CM 29697: posterior zygopophyses of an anterior lumbar vertebra.

cf. *Odocoileus virginianus* Zimmerman—
White-tailed Deer

MATERIAL: CM 29698: left naviculocuboid. 2 thoracic spines,

1 partial third or fourth cervical vertebra.

REMARKS: Identifications are tentative, based upon size comparisons with Recent material. These fragments may have been introduced by Recent woodrat activities, although signs of extensive gnawing were not noted. White-tailed deer are common in the area today. Both elk and deer remains have been reported from prehistoric Indian sites in Bath County approximately 11 km west of the cave

(MacCord, 1973a, 1973b).

Caribou (*Rangifer tarandus*) are known to have inhabited the Ridge and Valley section of the Appalachians as far south as Tennessee during the late Pleistocene (Guilday *et al.*, 1975) and may have been sympatric with both deer and elk during certain phases of glacial recession. No caribou remains were identified from the Clark's Cave deposit.

Table 20. Measurements (in mm) *Mustela erminea* and *Mustela nivalis*, Clark's Cave.

Species	\bar{X}	OR	N
Species	length, C - M1		
<i>M. erminea</i>	12.1	12.1	2
	length, P4		
<i>M. erminea</i>	4.4	4.0–4.7	5
<i>M. nivalis</i>	3.36	2.8–3.7	8
	width, P4		
<i>M. erminea</i>	2.12	2.0–2.3	5
<i>M. nivalis</i>	1.75	1.5–2.0	8
	width, M1		
<i>M. erminea</i>	3.65	3.6–3.7	2
<i>M. nivalis</i>	2.65	2.6–2.7	2
	length, m1		
<i>M. erminea</i>	4.2	3.9–4.6	4
<i>M. nivalis</i>	3.48	3.2–3.8	7
	width, m1, talonid		
<i>M. erminea</i>	1.22	1.2–1.3	4
<i>M. nivalis</i>	1.0	0.9–1.1	7

Measurements by Dr. Elaine Anderson.

FAUNAL COMPARISONS—METHODS OF DEPOSITION

The fossil faunas of two mid-Appalachian late Pleistocene small mammal deposits, New Paris No. 4, Pa., and Clark's Cave, Va., represent a sufficient number of individual animals to make statistical comparison possible. Both deposits sampled the same regional fauna in the same physiographic area, the Ridge and Valley section of the mid-Appalachians, during approximately the same time interval. The method of deposition was not the same, however.

At New Paris No. 4, Pa., mammals were trapped by falling down a narrow, vertical fissure 10 m in depth, which filled with accumulating surface debris.

At Clark's Cave, most mammal remains represent digestive remains, from raptorial birds, deposited on the talus floor in a sheltered cave entrance.

Despite the different methods of deposition, both faunas were composed almost exclusively of small mammals up to the size of a hare (98% at New Paris No. 4, 99.5% at Clark's Cave). In the former instance, size of entrapped mammals was governed by the small 1.5 m² entrance, in the latter by the selective bias of the Clark's Cave birds of prey. A casual size analysis of entrapped animals from the two faunas would give no indication of their differing modes of

deposition.

The proportion of small-to-large mammals in a raptor deposit is due to the selection bias of the birds of prey, and is independent of the time involved in forming such a deposit. The proportion of small-to-large mammals in a tumble-in trap, like a sinkhole, will increase with time. The slower the rate of infill, the greater the proportion of small-to-large mammals, because of their overwhelming majority in the surrounding fauna. This majority increases their probability of entrapment.

Bat remains were common at both deposits (43% MNI, New Paris No. 4; 36% MNI, Clark's Cave, Va.) but for different reasons. The New Paris No. 4 remains represent natural mortality of a resident population accumulating as infill progressed. The Clark's Cave bats were raptor prey. Bats are usually rare in owl pellet debris, and their presence in such numbers at the Clark's Cave roost reflects the special case of an owl roost situated at the mouth of a large cave containing a flourishing bat population. The numbers of bats at New Paris No. 4 and Clark's Cave do not reflect the difference in the method of deposition at the two sites. There are two clues, however: (1) The sinkhole bat material was exceptionally well-preserved, yielding complete skulls and semi-articulated remains, contrasting with the fragmented collection from Clark's Cave; (2) The New Paris No. 4 sample from a relatively small roost-shaft was dominated by only two species of *Myotis*, with a few *Pipistrellus* and *Eptesicus*. There were at least seven species of bats and five genera in the Clark's Cave deposit, a reflection of the much larger bat roosting area afforded by Clark's Cave and cliffs.

There are minor differences in the composition of the mammalian faunas from the two sites. Those small mammals most suitable for owl prey (shrews, moles, small rodents) were somewhat more common at Clark's Cave (see Table 21), but larger prey items (hares, rabbits) were relatively scarce. Lagomorphs were twice as common in the sinkhole deposit. These differences reflect the selection bias of the raptors. On the basis of these data alone the method of deposition is not apparent.

If one looks at the diversity of the two faunas, more obvious differences appear. Although all major mammal taxa are represented in both faunas, 54 species of mammals were identified from Clark's Cave, but only 40 from New Paris No. 4. The sinkhole sample was derived only from those animals blundering into the small surface opening, while the raptor-accumulated Clark's Cave deposit represents

a sampling from many habitats within the cruising range of the birds of prey.

Three other differences in relative numbers are noteworthy—many birds, few snakes, and presence of fish in the raptor roost deposit, compared with the sinkhole trap.

Birds are rarely trapped in vertical fissures, but are common in raptor debris. Two hundred and nineteen birds, of 68 species, 4.8% MNI of combined birds and mammals, were identified from Clark's Cave. At Natural Chimneys, Va., a probable roost site, similar to Clark's Cave, (79 birds, 40 species, or 9.33% of combined birds and mammals), birds were also a common element. In contrast, only nine birds representing seven species, or 0.3%, were present in the New Paris No. 4 sinkhole deposit, a ratio of one bird for every ten in the Clark's Cave deposit.

There was also a discrepancy in relative numbers of snake remains. Minimum numbers of individuals were not accurately ascertained but the number of snake vertebrae compared to the minimum number of mammals from the two sites was 39.1% at Clark's Cave, but 70.9% at New Paris No. 4. There was also a difference in the size of the individual snakes involved. Those at Clark's Cave were small and crotalids were not represented (with the possible exception of one fragmentary vertebra). At New Paris No. 4, however, snakes varied in size from what must have been new-born to large individuals, both colubrids and crotalids. Snakes were a minor food item at Clark's Cave. The raptors avoided large snakes. At New Paris No. 4, however, there was no such selection mechanism and, at least in the upper portions of the fissure deposit, snakes may have sought out the fissure for hibernation.

Turtle and lizard remains in both faunas were either not represented or were negligible. In the case of the turtles at New Paris No. 4 this is probably a reflection of late Pleistocene boreal conditions at the time of infill, for box turtles (*Terrapene carolina*) were common in neighboring sinkholes on the same hillside holding Recent faunal remains. The absence of turtles in an owl roost deposit may be due to raptor selection.

Frogs and toads were common to both sites (6.7% MNI Clark's Cave, 4.9% MNI New Paris No. 4, relative to MNI mammals).

To summarize: On the basis of the bone collections alone, and with no knowledge of the geological situation it is doubtful that one could state that New Paris No. 4 was a sinkhole trap deposit

while Clark's Cave was a raptor roost. There are a few differences, but they are relative and mostly take on meaning through hindsight. As more of these

faunas are studied, however, the differences noted above may take on greater significance.

Table 21. Mammal composition of two mid-Appalachian cave deposits.

MAMMALS	New Paris No. 4, Pa. Sinkhole Trap			Clark's Cave Raptor Roost		
	Number of Species	Number of Individuals	Per cent of Individuals	Number of Species	Number of Individuals	Per cent of Individuals
Talpidae – moles	2	3	.10	3	26	.50
Soricidae – shrews	7	107	3.74	7	231	5.30
Chiroptera – bats	4	1235	43.22	8	1554	35.78
Sciuridae – squirrels	6	83	2.90	8	117	2.69
Cricetidae – deer mouse, woodrat	3	238	8.33	3	272	6.26
Arvicolidae – voles	10	1213	42.57	9	2060	47.43
Zapodidae – jumping mice	2	17	.59	2	37	.85
Erethizontidae – porcupine	1	3	.10	1	1	.02
Leporidae – rabbits	1	52	1.82	2	24	.55
Carnivora – carnivores	3	5	.17	8	19	.44
Artiodactyla – hoofed animals	1	1	.03	2	2	.04
Totals – Mammal	40	2857		53	4343	
BIRDS	7	9		68	210	
% Total birds to total mammals			.31			4.83

ECOLOGICAL INTERPRETATION

The interpretation of the fauna of the Clark's Cave fossil deposit is clouded by three factors: (1) selective bias of the carnivorous birds responsible for the deposit (influenced by variations in hunting techniques, species of raptors, time of the year roost was occupied, size of prey, hunting radius); (2) great

topographic diversity providing a variety of environmental niches; (3) lack of definite knowledge of the time interval represented by the deposit within the rapidly changing framework of late glacial times.

BIRD SUMMARY

Eighty-five species of birds have been reported from three late Pleistocene cave deposits in Virginia: Clark's Cave; Back Creek Cave No. 2, Bath County; and Natural Chimneys, Augusta County. Nine species were common to all three deposits: spruce grouse, *Canachites canadensis*; ruffed grouse, *Bonasa umbellus*; sharp-tailed grouse, *Pedioecetes phasianallus*; bobwhite, *Colinus virginianus*; woodcock, *Philohela minor*; passenger pigeon, *Ectopistes migratorius*; flicker, *Colaptes auratus*; blue jay, *Cyanocitta cristata*; and junco, *Junco hyemalis*. Seventeen additional species were present in at least two of the deposits: blue-winged teal, *Anas discors*;

sharp-shinned hawk, *Accipiter striatus*; broad-winged(?) hawk, *Buteo platypterus*; American kestrel, *Falco sparverius*; rock(?) ptarmigan, *Lagopus cf. mutus*; turkey, *Meleagris gallopavo*; kingfisher, *Megasceryle alcyon*; red-headed woodpecker, *Melanerpes erythrocephalus*; hairy woodpecker, *Dendrocopos villosus*; downy woodpecker, *Dendrocopos pubescens*; cliff swallow, *Petrochelidon pyrrhonota*; gray jay, *Perisoreus canadensis*; red-breasted nuthatch, *Sitta canadensis*; brown thrasher, *Toxostoma rufum*; robin, *Turdus migratorius*; red-winged blackbird, *Agelaius phoeniceus*; pine grosbeak, *Pinicola enucleator*.

Undue emphasis should not be placed on the presence or absence of a given species of bird, because of predator bias and identification problems inherent in the relatively poor preservation of fragile bird bones. The 26 species listed above were common enough in western Virginia during late Pleistocene times to have appeared in more than one site.

All three sites occur in the intermontane valleys of western Virginia and are roughly comparable in age. The avian fauna complements the paleoecological picture suggested by the mammals. The presence of such relatively sedentary birds as spruce grouse, sharp-tailed grouse, and ptarmigan suggests cooler conditions and an open coniferous parkland—a picture complicated by the topographic diversity of the region, probably presenting a mosaic of open and closed situations.

Only the three species of grouse and the passenger pigeon were present in substantial numbers, a situation that may reflect the collecting bias of the raptors responsible for the deposit rather than their true relative abundance. Ptarmigan and passenger pigeon [although the latter formerly occurred seasonally as far north as James Bay, ca. 52° N. latitude (Todd, 1963)] were not normally found in any numbers in

the same area within historic times. Their co-presence at Clark's Cave and Back Creek No. 2, assuming they were contemporaneous in the area, which is most likely, was due to the ecological diversity imposed by the mountainous terrain and the ability of birds, both predator and prey, to transgress the bounds of their "normal" habitats, especially if contiguous habitats like open, tundra-like ridge crests and more heavily wooded intermontane valley parklands or bog-forests were to parallel each other throughout the central Appalachians during glacial maxima.

The sharp-tailed grouse and the magpie (*Pica pica*), the latter found only at Natural Chimneys, represent former eastern extensions of their present western ranges (see Fig. 14). Neither species is found in a closed-forest situation today. Their presence suggests semi-prairie or parkland conditions and reinforces a similar conclusion from western elements in the mammal fauna:—13-lined ground squirrel and least chipmunk. There have been undated, but presumably late Pleistocene, finds of badger, *Taxidea taxus*, (Bootlegger Sink, Pa., CM collection, unpublished) and grizzly bear, *Ursus arctos*, (Organ Cave, W. Va., CM 12999) that fit this picture as well.

MAMMAL SUMMARY

Within Recent times 68 species of mammals are known to have inhabited the mid-Appalachians (Table 22, columns 2 and 3). Fifty-four species were identified from the cave deposit (Table 22, columns 1 and 2). Those Recent mammals missing from the deposit were either too large or formidable (*Bison bison*, *Felis concolor*, *Lynx rufus*, *Martes pennanti*, *Lutra canadensis*, *Canis lupus*, *Vulpes vulpes*, *Urocyon cinereoargenteus*, *Castor canadensis*) to be taken by most raptors, or were of "southern" distribution (?*Sorex longirostris*, *Cryptotis parva*, *Sylvilagus floridanus*, *Sciurus niger*, *Reithrodontomys humulis*, *Ochrotomys nuttalli*, *Mustela frenata*, *Spilogale putorius*). The absence of the hoary and silver-haired bats (*Lasiurus cinereus*, *Lasionycteris notivagans*) is not surprising considering their migratory habits and rarity in and around caves. Three Recent rodents, black rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*), house mouse (*Mus musculus*), Old World forms introduced during the Colonial period, were also absent. Considering its present abundance and its paleogeographic his-

tory, the absence of opossum (*Didelphis virginianus*) remains from the site is probably significant. Although reported from the late Pleistocene of Devil's Den, Fla., and Ladds Quarry, Ga., opossum remains have been conspicuously absent from all eastern North America deposits of that period from East Tennessee to Pennsylvania. Even as late as the 16th century, based upon analyses of aboriginal cultural debris (Guilday, 1958), *D. virginianus* was rare or absent in the Northeast, and its spread north to southern Canada and New England was a relatively recent phenomenon. *Sylvilagus floridanus*, *Sciurus niger*, *Reithrodontomys* and *Ochrotomys*, based upon their present distributions, seem out of place in a late-glacial boreal setting, and were probably not in the area at the time the deposit was accumulating.

Nine species of mammals found in the deposit do not inhabit the mid-Appalachians today. The dire wolf (*Canis dirus*) is extinct. The remaining eight are all of boreal or mid-Western affinities (*Sorex arcticus*, *Eutamias minimus*, *Spermophilus tridecemlineatus*,

Synaptomys borealis, *Phenacomys intermedius*, *Microtus xanthognathus*, *Mustela erminea*, *Martes americana*).

If we omit mammals not reasonably considered raptor prey—those species larger than a woodchuck (3 kg±)—thus reducing the selective bias introduced by predator preference, 48 species of medium-to-small-sized mammals were identified from the fossil deposit. Eight of these (16.6%, see above) no longer occur in the mid-Appalachians. An additional 11 (25%) survive at that latitude, at higher elevations in the mountains, and have not been found in the Cowpasture valley (*Condylura cristata*, *Parascalops breweri*, *Sorex cinereus*, *Sorex palustris*, *Peromyscus maniculatus*, *Clethrionomys gapperi*, *Microtus chrotorrhinus*, *Napaeozapus insignis*, *Sylvilagus transitionalis*, *Lepus americanus*, and *Glaucomys sabrinus*). An additional five (10.4%), although still living near the site today, differ in size characteristics from their modern counterparts, agreeing with modern boreal samples of the same species or with those from the late Pleistocene New Paris No. 4 fossil collection (*Blarina brevicauda*, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Glaucomys volans*, and *Synaptomys cooperi*).

The mammalian fauna of the Clark's Cave deposit is almost identical with that of New Paris No. 4, Pa. Differences can be ascribed to its more southerly location (absence of *Dicrostonyx*, higher numbers of *Sorex fumeus*, *Microtus pinetorum*, and *Peromyscus leucopus*), possible accidents of deposition and sampling (presence of *Eutamias minimus* at Clark's Cave, but not at New Paris No. 4), or predator bias (absence of *Mylohyus* and larger variety of bats at Clark's Cave). The activity of raptors was also apparent in the greater number of birds from Clark's Cave. Those boreal forms represented at Clark's Cave but not at New Paris No. 4,—ptarmigan, spruce grouse, gray jay—may simply not have been trapped in the tumble-in sinkhole at New Paris No. 4.

The bulk of the recovered fauna, as at New Paris No. 4, suggests that the predominate vegetative cover was an open boreal woodland dominated by conifers. Topographical diversity undoubtedly produced, as it does today, a variety of ecological niches. The only significant difference between the two faunas was the presence of the collared lemming, *Dicrostonyx hudsonius*, at New Paris No. 4, Pa., but not at Clark's Cave. As the Clark's Cave raptors concentrated on voles as a major prey item, the absence of the collared lemming at Clark's strongly suggests the absence of paucity of tundra in the Cowpasture valley

or its neighboring mountain walls. Tundra conditions somewhere in the area are suggested by the presence of bones of the more vagile ptarmigan both at Clark's Cave and at Back Creek Cave No. 2, 24 km to the west. The evidence to date suggests that while tundra may have extended down the Appalachians to at least the latitude of New Paris No. 4, Pa. (*Dicrostonyx*) and Buckle's Bog, Md. (pollen profile, Maxwell & Davis, 1972), its presence as far south as west-central Virginia may have been discontinuous.

In common with the mammals recovered from Clark's Cave, no species of bird found solely to the south of Virginia today was recovered. All species occur in the state today or farther to the north and northwest (spruce grouse, sharp-tailed grouse, gray jay, pine grosbeak, and rock (?) ptarmigan). In summary, the recovered mammal fauna agrees in its ecological implications with the bird fauna in the absence of "southern" species and the influx of northern and western forms.

A shortcoming of a fossil raptor roost like the Clark's Cave deposit, is the virtual absence of large mammals because of the selection bias of the birds. There are large late Pleistocene mammals known from western Virginia in local faunas, unaccompanied by smaller vertebrates, so that the fuller picture must be pieced together from several sites that may or may not have been exactly contemporaneous. Ground sloth, *Megalonyx*; mammoth, *Mammuthus primigenius*; mastodon, *Mammuthus americanus*; horse, *Equus*; caribou, *Rangifer tarandus*; extinct moose, *Cervalces*; bison, *Bison*; extinct muskoxen, *Symbos* and *Bootherium*; have been recovered from Saltville, Smyth County, Va., southwest of Clark's Cave, associated with a date of 13,460 radiocarbon years. The pollen associated with the muskox remains (Ray *et al.*, 1967) indicated a flora dominated by spruce and pine, and was interpreted as spruce parkland interspersed with ponds, marshes, and prairies, an environment similar to that suggested by the Clark's Cave local fauna. These large herbivores were attracted to and mired in saline springs. Molars of the giant beaver (*Castoroides ohioensis*) have been recovered from Natural Chimneys, Va. Long-nosed peccary *Mylohyus nasutus* is known from Natural Chimneys and Back Creek No. 1, Va. There is archaeological evidence from Russell Cave, Ala., that *Mylohyus nasutus* may have survived as late as 7,000 years ago. No direct evidence links any of these large animals with the Clark's Cave local fauna, but they probably coexisted with it.

Table 22. Species of mammals, Clark's Cave, and Recent mid-Appalachians. () = MNI, fossil deposit.

Present in Clark's Cave deposit only	Present in Clark's Cave deposit and Recent mid-Appalachians	Present in Recent mid-Appalachians only
	Family Didelphiidae	
		<i>Didelphis virginianus</i>
	Family Talpidae	
	<i>Condylura cristata</i> (13)	
	<i>Parascalops breweri</i> (12)	
	<i>Scalopus aquaticus</i> (1)	
	Family Soricidae	
<i>Sorex arcticus</i> (13)	<i>Sorex cinereus</i> (67)	<i>Sorex longirostris</i>
	<i>Sorex dispar</i> (4)	
	<i>Sorex fumeus</i> (10)	<i>Cryptotis parva</i>
	<i>Sorex palustris</i> (7)	
	<i>Microsorex hoyi</i> (7)	
	<i>Blarina brevicauda</i> (97)	
	Family Vespertilionidae	
	<i>Myotis lucifugus/sodalis</i> (c. 877)	<i>Lasionycteris noctivagans</i>
	<i>Myotis keenii</i>	
	<i>Myotis leibii</i> (c. 138)	<i>Lasiurus cinereus</i>
	<i>Myotis grisescens</i> (c. 138)	
	<i>Eptesicus fuscus</i> (363)	
	<i>Pipistrellus subflavus</i> (26)	
	<i>Plecotus townsendii</i> (9)	
	<i>Lasiurus borealis</i> (3)	
	Family Leporidae	
	<i>Lepus americanus</i> (23)	<i>Sylvilagus floridanus</i>
	<i>Sylvilagus transitionalis</i> (1)	
	Family Sciuridae	
<i>Eutamias minimus</i> (3)	<i>Tamias striatus</i> (24)	<i>Sciurus niger</i>
<i>Spermophilus tridecemlineatus</i> (5)	<i>Marmota monax</i> (2)	
	<i>Tamiasciurus ludsonicus</i> (25)	
	<i>Sciurus carolinensis</i> (3)	
	<i>Glaucomys volans</i> (19)	
	<i>Glaucomys sabrinus</i> (28)	
	Family Castoridae	
		<i>Castor canadensis</i>
	Family Cricetidae	
	<i>Peromyscus maniculatus</i> (c. 117)	<i>Reithrodontomys humulis</i>
	<i>Peromyscus leucopus</i> (c. 104)	<i>Ochrotomys nuttalli</i>
	<i>Neotoma floridana</i> (51)	
	Family Arvicolidae	
<i>Synaptomys borealis</i> (61)	<i>Synaptomys cooperi</i> (23)	
<i>Phenacomys intermedius</i> (34)	<i>Clethrionomys gapperi</i> (305)	
<i>Microtus xanthognathus</i> (511)	<i>Microtus pennsylvanicus</i> (c. 658)	
	<i>Microtus chrotorrhinus</i> (c. 292)	
	<i>Microtus pinetorum</i> (170)	
	<i>Ondatra zibethicus</i> (6)	

Table 22. Species of mammals, Clark's Cave, and Recent mid-Appalachians. () = MNI, fossil deposit (continued).

Present in Clark's Cave deposit only	Present in Clark's Cave deposit and Recent mid-Appalachians	Present in Recent mid-Appalachians only
	Family Muridae	
		<i>Rattus rattus</i> <i>Rattus norvegicus</i> <i>Mus musculus</i>
	Family Zapodidae	
	<i>Zapus hudsonius</i> (22) <i>Napaeozapus insignis</i> (15)	
	Family Erethizontidae	
	<i>Erethizon dorsatum</i> (1)	
	Family Canidae	
<i>Canis cf. dirus</i> (1)		<i>Canis lupus</i> <i>Vulpes vulpes</i> <i>Urocyon cinereoargenteus</i>
	Family Ursidae	
	<i>Ursus americanus</i> (1)	
	Family Procyonidae	
	<i>Procyon lotor</i> (1)	
	Family Mustelidae	
<i>Martes americana</i> (1) <i>Mustela erminea</i> (4)	<i>Mustela nivalis</i> (7) <i>Mustela vison</i> (2) <i>Mephitis mephitis</i> (1)	<i>Martes pennanti</i> <i>Mustela frenata</i> <i>Spilogale putorius</i> <i>Lutra canadensis</i>
	Family Felidae	
		<i>Felis concolor</i> <i>Lynx rufus</i>
	Family Cervidae	
	<i>Cervus elaphus</i> (1) <i>Odocoileus virginianus</i> (1)	
	Family Bovidae	
		<i>Bison bison</i>

AGE OF DEPOSIT

It is clear, from the presence of so many boreal birds and mammals, that the deposit accumulated during a cooler climatic episode. The mammalian fauna, with minor exceptions, is identical with that of New Paris No. 4, Pa. (11,000 years B.P.), even to infraspecific size (Bergmann's Response). This, plus the relatively superficial nature of the deposit

scattered throughout the upper 45 cm of an unconsolidated cliff talus, indicates a relatively late date, but one predating the Recent fauna and flora.

Deposition could not have extended very far, if at all, into Recent times on a sustained basis. In addition to the negative evidence of the absence of introduced or domestic species of birds and mammals, the

size characteristics of the fossil population samples of species like *Sorex cinereus*, *Blarina brevicauda*, *Condylura cristata*, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Glaucomys volans*, *Glaucomys sabrinus*, *Lepus americanus*, *Synaptomys cooperi*, and *Napaeozapus insignis* are distinct from their Recent mid-Appalachian representatives, paralleling those of New Paris No. 4, Pa. If deposition at the site had continued into Recent times there should have been a size-continuum between the late Pleistocene and Recent representatives within each species, expressed as an increase in variation, larger observed ranges, and higher coefficients of variation. Such was not the case. Deposition must have halted, for all practical purposes, before these mammals showed any degree of measurable physiological adjustment to the changing environment.

Judging from the rate of accumulation of modern "owl-roosts," the Clark's Cave deposit was built up in a relatively short time, probably between 20,000 and 11,000 years ago—a concentrated accumulation of an active population of both adult and fledgling raptors. Deposition may have been terminated by rockfalls, but this is not apparent at the site today, and the deposit was not buried under rock debris. The abandonment of the roost as a nesting site may have been hastened by Indian molestation in this easily accessible river-bank nesting site. Wayne C. Clark, Assistant Archaeologist, Archaeological Society of Virginia (letter, Oct. 1, 1975) reports 32 Prehistoric Indian sites from Bath County alone, dating primarily from 8,000 B.C. to 1,600 A.D., with the majority of the large sites dating to the Woodland period, ca. 1,000 B.C. to 1,600 A.D., so that the Clark's Cave raptors could have been subject

to human predation for at least the last 10,000 years. This is speculation, however. Any evidence of a prehistoric occupation in any of the larger entrances of Clark's Cave would have been destroyed by the Colonial and Civil War saltpeter miners.

If we assume that deposition ceased at the site prior to Recent times, there are a few seeming anomalies—the presence of the woodland vole (*Microtus pinetorum*) and the white-footed mouse (*Peromyscus leucopus*) in greater numbers than one would expect in a boreal environment suggests either that they were able to adjust to the periglacial conditions at this latitude or, perhaps, were pioneer colonizers in the ecological ferment of post-glacial warming. Both species are inhabitants of dry, deciduous, hardwood forests, but occur locally in northern New England today in cool hemlock/maple woods of Canadian aspect. The presence of a single individual of the eastern mole (*Scalopus aquaticus*) appears anomalous, based on its present geographic distribution, as well as of birds like the bobwhite, *Colinus virginianus* (two individuals), and one individual each of orchard oriole *Icterus spurius*, tanager *Piranga* ?species, and a questionable red-bellied woodpecker *Centurus carolinus*. Owls still roost on the Clark's cliffs, however, and a scattering of Recent remains may have been introduced into the deposit.

A C14 date of 2,260±85 years B.P., based on bone carbonate, was obtained from a sample of 215 gms of unsorted bone fragments (I-7224). This date is obviously too recent. The superficial nature of the deposit increased the chances of contamination and the date is unacceptable as far as dating the Clark's Cave deposit is concerned.

THE LATE GLACIAL ENVIRONMENT

Late glacial climatic changes and their biological consequences are still known only in broadest outline. Data have accumulated from geological and biological sources, both marine and terrestrial—frost and ice phenomena, plant fossils including pollen, invertebrate and vertebrate fossils—that point to effects of glacial cooling extending to lower latitudes hundreds of kilometers south of the terminal Wisconsinan moraine.

The extent and direction of environmental change in the Appalachians is governed by the regional topography—long, parallel mountain ridges inter-

persed with intermontane valleys extending southwards in essentially unbroken array from the former glacial front to the Carolinas and Georgia, culminating in the Great Smoky Mountains. The effect of such topography is seen today in the distribution of forest types.

"... The long southward projection of the northern hardwood forests on the Appalachian summits today probably had a full glacial predecessor in the form of tundra and boreal forest. Such a projection could have been a main avenue for the invasion of boreal elements into the boreal forests

of the time." (Flint, 1971:509)

Evidence of glacial cooling reflected in the distribution of boreal species of plants during full glacial times (Watts, 1970) has been recorded from as far south as Georgia and northern Florida. We will concentrate on climatic changes in the central Appalachian West Virginia/Virginia area and their relationship to Clark's Cave (see V. A. Carbone's excellent survey of the late-glacial environment in the neighboring Shenandoah Valley, Va., in Gardner, 1974:84-99).

There is evidence from several sources for the former occurrence of Wisconsinan-age tundra, *i.e.*, open, treeless grass and sedge expanses and permafrost in the Appalachian highlands south of the terminal moraine. The most dramatic claim, former alpine glaciation at Boone Fork, Grandfather Mountain, N.C. at 36° O' N. (Berkland & Raymond, 1973), has been rejected. It was based upon parallel grooves, worn into rock outcrops by metal logging cables, that were misinterpreted as glacial striations (McKeon, 1974; Hack & Newell, 1974; Berkland & Raymond, 1974). But the presence of block fields and of patterned-ground relicts on ridge crests from Pennsylvania to southern Virginia at altitudes ranging from 707 m in central Pennsylvania (Riansares) to 1,615 m (Whitetop Mountain) on the Tennessee/Virginia/North Carolina border (Clark, 1968, in Flint, 1971:283) suggests former permafrost activity. These sites are undated and may conceivably have predated the Wisconsinan glaciation. Direct evidence of Wisconsinan age tundra in the central Appalachians rest upon the evidence of plant and animal fossils. A pollen profile extending back into full glacial times is known from Buckle's Bog, Md., at the headwaters of the Casselman River, at an elevation of 814 m, 170 km north of Clark's Cave on the eastern rim of the Appalachian Plateau. Maxwell and Davis (1972), studied a 258 cm core from Buckle's Bog and interpreted the lowermost 66 cm (zone BB-1), dated from 19,000 to 12,700 radiocarbon years, as true tundra. Nonarboreal pollen, over 50% sedges and grasses, predominated. Spruce (10-22%) and pine (5-17%) were the dominant arboreal pollen. The authors construed the relatively high percentage of spruce to pine as indicative of the nearby spruce, perhaps in sheltered valleys within 25 km of the site. Pine pollen, shed in greater abundance and more widely wind-distributed, should have been present in greater relative amounts if spruce were not locally present.

The faunal evidence for the former presence of

tundra, although not as extensive as that obtained from pollen analysis, is highly suggestive. Direct historical continuity between the Wisconsinan low-latitude periglacial tundra and the Recent eastern Canadian tundra is indicated by the skeletal remains of the Hudson's Bay collared lemming, *Dicrostonyx hudsonius*, at 11,300 radiocarbon years, from New Paris No. 4, Pa., at the relatively low altitude of 465 m, just 16 km east of the rim of the Appalachian Plateau. The ptarmigan, *Lagopus* sp., reported in this paper from Clark's Cave and nearby Back Creek No. 2 Cave, also suggests the near presence of tundra or tundra-like conditions. Because birds are more mobile than mammals and the possibility exists that the ptarmigan may be the willow rather than the rock ptarmigan, the evidence is not as firm as at New Paris No. 4. But at least, nearby open ground is indicated. Other boreal species, recorded from cave deposits as far south as 36° latitude in Tennessee (the caribou, *Rangifer tarandus*), 34° latitude Georgia (the spruce grouse, *Canachites canadensis*), and porcupine from the Coleman IIA fauna, Fla., 29° latitude, indicate just how far south mammalian adjustments occurred.

Changes in forest composition following the Wisconsinan glacial recession were first noted at about 13,600 radiocarbon years as a shift from coniferous to deciduous species in Georgia. But, on the basis of radiocarbon dating, approximately 1,000 more years were required for floral changes to be noted in the higher and more northern Appalachian plateau and ridge provinces as a change from tundra vegetation to boreal woodland (Maxwell & Davis, 1972). The situation at Clark's Cave at this time was somewhat different. The broad expanse of the Appalachian Plateau flanking the northwestern approaches to the Appalachian ridges served as a wind and precipitation shield between them and the continental glaciers (Fig. 2 insert). Consequently the intermontane valleys to the east were protected from the full climatic rigors of the period. Pollen analyses at Hack and Querles ponds, on the floor of the Shenandoah valley, near Staunton, Va. (Craig, 1969), indicate that at the time tundra was noted at Buckle's Bog and, by extension, from the higher ridges of the Appalachian Plateau and Mountains, the protected valley floors supported an open spruce and pine woodland. And as the tundra gave way to open spruce woodland in the higher Alleghenies between 12,700 and 10,000 radiocarbon years, the spruce woodlands of the protected intermontane valleys were changing to mixed closed-canopied forests

of spruce, pine and hardwoods.

The late Pleistocene vegetation of the Clark's Cave area during the deposition of the fossil deposit is hard to categorize because of the rugged terrain. Local topographical relief is some 500 m within a few kilometers of the site. Topography varies from flat flood plain to cliff and mountainous terrain. The picture derived from the fauna itself can only be a montage, but full glacial conditions in the Cowpasture River valley can be visualized as a spruce parkland. The flood plain was probably dotted with copses of spruce intermingled with prairie, marshes, and small ponds. The shale hills along the eastern margin of the river valley that now support a xeric shale-barren flora were, in all probability, relatively dry then, perhaps supporting jackpine (*Pinus banksiana*) parklands. The presence of marshes or small standing-water ponds is suggested by grebes, bitterns, ducks, rails, plovers, and sandpipers, (26% of the identified species of birds from the deposit) and the number and variety of frogs.

Coniferous to deciduous change in forest composition proceeded with great rapidity. This was reflected in the changing make-up of the vertebrate fauna. Most of the mammals present during boreal times either migrated to higher latitudes, underwent physiological adjustment, or especially in the case of the larger species, became extinct. Three carbon dates associated with mammalian faunas in Pennsylvania are relevant. At 11,300 radiocarbon years, the fauna of New Paris No. 4, Pa., was dominated by boreal small rodents and insectivores. By 8,570 radiocarbon years, the fauna from New Paris sinkhole No. 3 at New Paris, situated within a few meters of sinkhole No. 4, was a Recent one with no trace of the boreal species that so dominated the latter site. The mammalian fauna associated with a date of 9,240 radiocarbon years at Hosterman's Pit, Pa., 136 km northeast of New Paris, was likewise Recent in species composition. This suggests that a radiogenically undated deposit like that at Clark's Cave can be assigned a rather definite age limit (minimum if boreal in make-up, maximum if composed of Recent species).

Following the period of initial coniferous/decid-

uous floral turnover, the region has been characterized by a closed-canopy, oak-dominated deciduous forest. There have been minor climatic changes reflected in relative forest composition, successive submaxima of hemlock (*Tsuga*), chestnut (*Castanea*), and hickories (*Carya*) that probably required little, if any, adjustment on the part of at least the larger mammals. Changes of this magnitude may not be monitored by deposits like the Clark's Cave fossil assemblage that are not as sensitive as pollen sites to minor climatic oscillations.

The Clark's Cave local fauna with its mixture of forest and meadow forms and its boreal, continental aspect suggests several distinct habitats within the hunting radius of the cave-based raptors. The climatic model of Saltzman and Vernekar (1975) suggests that the Full Glacial averaged macroclimate of the Holarctic ice border was cold and dry with reduced precipitation and evaporation. Channel-scouring and downcutting in late glacial fluvial deposits of the South Fork Potomac River, northeast of Clark's Cave, suggests increased stream velocity and run-off attributed to decreased evaporation (Gardner, 1974).

This suggests that the floor of the Cowpasture River valley may have been relatively more mesic than the surrounding high-relief uplands because of a higher regional water table and the pooling of slope run-off caused by lower evaporation rates. The extensive flood plain (Fig. 10) probably developed boreal bogs and grass and sedge wetlands, while the relatively xeric uplands supported coniferous scattered woodlands, their density depending upon local hydrologic conditions. Such an environment would satisfy the mixed requirements of the varied fossil assemblage, allowing the raptors to draw from contiguous but contrasting habitats.

The most disturbing aspect of the deposit is the lack of an absolute date within the Wisconsin late glacial period. Only one fully comparable deposit has been studied in the area, New Paris No. 4, Pa. Perhaps this will remedy itself when more sites are developed and temporal faunal changes with refugial survivals are documented in the mid-Appalachians during the late Pleistocene.

LIFE ZONE INTEGRITY

The view that periglacial biotic adjustment to continental glacial oscillations was essentially just latitudinal and altitudinal shifting of present life-

zone systems is no longer tenable. The initial picture presented by pollen analysis could evoke several interpretations because it was possible to study only

Table 23. Site References.

Site	Age	Type of Site	Reference
Alabama			
Russell Cave	c. 7 – 9,000 yrs. B.P.	Cave	Weigel <i>et al.</i> , 1974
Arkansas			
Conard Fissure	Irvingtonian	Cave, fissure	Graham, 1972; Brown, 1908
Peccary Cave, Newton Co.	2,230 \pm 120 yrs. B.P. 16,700 \pm 250 yrs. B.P.	Cave	Davis, 1969; Quinn, 1972; Semken, 1969
Florida			
Coleman IIA, Sumter Co.	"Middle Pleistocene"	Sinkhole	Martin, 1974
Devil's Den, Levy Co.	Late Pleistocene/early Holocene	Sinkhole	Martin & Webb, 1974
Georgia			
Ladds Quarry, Bartow Co.	Rancholabrean	Fissure	Ray, 1965, 1967; Lipps & Ray, 1967; Wetmore, 1967
Idaho			
Jaguar Cave, Lemhi Co.	10,370 \pm 350 yrs. B.P. 11,580 \pm 250 yrs. B.P.	Cave	Guilday & Adams, 1967; Kurten & Anderson, 1972
Wilson Butte, Jerome Co.	4,890 \pm 300 yrs. B.P. (M-1087) 15,000 \pm 800 yrs. B.P. (M-1410)	Cave	Gruhn, 1961, 1965
Illinois			
Meyer Cave, Monroe Co.	Early Holocene	Fissure	Parmalee, 1967
Iowa			
Brayton local fauna, Audubon Co.	12,420 \pm 180 yrs. B.P.	Fluvial	Dulian, 1975
Waubonsie local fauna, Mills Co.	"late Wisconsinan"	Fluvial	Hallberg <i>et al.</i> , 1974
Kentucky			
Welsh Cave, Woodford Co.	12,950 \pm 550 yrs. B.P. (I-2982)	Cave, sinkhole	Guilday <i>et al.</i> , 1971
Maryland			
Cumberland Cave, Allegany Co.	Irvingtonian	Cave, fissure	Gidley & Gazin, 1938
Minnesota			
Itasca Bison Site, Clearwater Co.	7 – 8,000 yrs. B.P.	Bison kill, Fluvial	Shay, 1971
Missouri			
Bat Cave, Pulaski Co.	Rancholabrean	Cave	Hawksley, <i>et al.</i> , 1973
Crankshaft Cave, Jefferson Co.	Late Pleistocene/Recent	Sinkhole	Parmalee, <i>et al.</i> , 1969
Pennsylvania			
Bootlegger Sink, York Co.	Rancholabrean/early Holocene	Cave, sinkhole	Guilday, <i>et al.</i> , 1966
Hosterman's Pit, Centre Co.	9,240 \pm 1,000 yrs. B.P. (M-1291)	Cave	Guilday, 1967
New Paris No. 2, Bedford Co.	1,875 \pm 100 yrs. B.P. (I-743)	Sinkhole	Guilday & Bender, 1958
New Paris No. 3, Bedford Co.	8,570 \pm 145 yrs. B.P. (I-5313)	Sinkhole	CMNH unpubl.
New Paris No. 4, Bedford Co.	11,300 \pm 1,000 yrs. B.P. (Y-727)	Sinkhole	Guilday <i>et al.</i> , 1964
Sheep Rock Shelter, Huntingdon Co.	490 \pm 100 yrs. B.P. (M-1904) 8,920 \pm 320 yrs. B.P. (M-1909)	Rockshelter	Guilday & Parmalee 1965; Michels & Smith, 1967
Tennessee			
Baker Bluff Cave, Sullivan Co.	10,560 \pm 220 yrs. B.P. } (GX 3370) 11,640 \pm 250 yrs. B.P. } 19,100 \pm 850 yrs. B.P. (GX 3495)	Cave, fissure	Guilday <i>et al.</i> , 1975
Guy Wilson Cave, Sullivan Co.	19,700 \pm 600 yrs. B.P. (I-4163)	Cave	Guilday <i>et al.</i> , 1975
Robinson Cave, Overton Co.	Rancholabrean	Cave	Guilday <i>et al.</i> , 1969
Virginia			
Back Creek Cave No. 1 (Cook Cave), Bath Co.	Rancholabrean	Rockshelter, owl roost	CMNH coll., unpubl.

Table 23. Site References (continued).

Site	Age	Type of Site	Reference
Virginia (continued)			
Back Creek Cave No. 2 (Sheets Cave), Bath Co.	Rancholabrean	Rockshelter, owl roost	CMNH coll., unpubl.
Natural Chimneys, Augusta Co. Saltville	Rancholabrean 13,460± 420 yrs. B.P. (SI-461)	Cave, owl roost Paludal	Guilday, 1962 Ray <i>et al.</i> , 1967

a portion of the fossil flora (those plants possessing identifiable wind-distributed pollen). Only a generalized conception of the sampled paleoenvironment was possible. Anomalous deciduous pollen present in an otherwise boreal pollen profile was always susceptible to the interpretation that it was not indigenous, but wind-transported from a distance. Remains of large Pleistocene mammals, mostly those of extinct herbivores (proboscideans, ovi-bovines, sloths, cervids) and carnivores could supply little to the detailed ecological picture.

Pollen analysis supplied the outlines of biotic adjustment in lower latitudes, and convincingly demonstrated that the magnitude of change was much greater than that suggested by earlier workers who lived prior to the advent of palynology as a research tool (Braun, 1950). But the question of the detailed biotic composition of these adjustments, whether they represented simple biome fluctuations or resulted in new and unique combinations, remained open until paleontological sites of late Pleistocene age, containing remains of ecologically sensitive small vertebrates of known Recent habitat, were discovered and analyzed.

Initiated in modern form by the late C. W. Hibbard (Hibbard, 1949), techniques for recovering micro-vertebrates soon demonstrated that periglacial faunas were composed of an amalgam of temperate and boreal species, and that the fossil faunas, even though composed of Recent forms, could not be duplicated today at any latitude. Initial analysis of such sites consisted of constructing overlap maps (like Fig. 18, this paper) in which the Recent ranges of the various recovered species were superimposed on one another and the area of maximum overlap was considered an approximation, or, at the least, an indication of former environments.

It is becoming obvious that modern boreal terrestrial environments cannot be considered analogous to late Pleistocene situations in lower latitudes. Even if the climate could be duplicated precisely, which is not possible, differences in topography, geology, and the historical development of their

respective biotas could not. Modern eastern North American boreal biotas are composed largely of post-Wisconsinan immigrants occupying deglaciated terrain that had been stripped of living things by glacial ice. Hence a competitive edge was given to those species preadapted for a harsh boreal environment and capable of rapid spreading. Southern periglacial faunas, on the other hand, were composed of both boreal forms and those temperate species that could survive either in local refugia or in various degrees of integration in an unglaciated situation. Periglacial habitats were not created and destroyed with the rapidity of those once covered by ice, but adjusted slowly and less dramatically with climatic change, creating a fluid mosaic of environmental niches supporting a richer biota than would be the case if that biota had to start anew (as in once-glaciated areas) with no historical continuity.

Work by Dr. Holmes Semken, University of Iowa, and his students on late Pleistocene faunas from the Midwest demonstrated that this is true even for areas of little topographic diversity. Although different species are involved, the picture becomes even more complicated in the Appalachian Mountains where highlands and lowlands parallel each other alternately for hundreds of kilometers in a north-south direction. The richness of the Clark's Cave local fauna, compared to the more boreal New Paris No. 4 fauna, 240 km to the north, appears to express this biotic gradient. In addition to this boreal-temperate intermesh, a cross-mesh of eastern forest and now mid-western forms occurred, producing a unique fauna that cannot be analyzed in the light of the present-day habitat requirements of each species taken individually. Each component species was responding not only to environmental pressures, but to pressures resulting from new and unique combinations of species, so that the definitive environmental picture of that time and place may not be the sum of its component parts as suggested by the Recent ecological requirements of each of the species involved.

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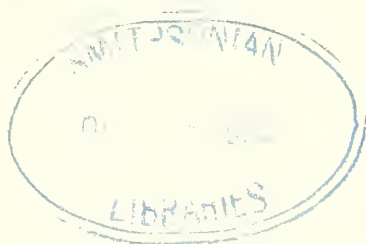




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BULLETIN

of CARNEGIE MUSEUM OF NATURAL HISTORY



THE CHACOAN PECCARY *CATAGONUS WAGNERI* (RUSCONI)

RALPH M. WETZEL

NUMBER 3

PITTSBURGH, 1977

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BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 3, pages 1-36, figures 1-10, tables 1-8

Issued June 29, 1977

Price \$6.00 a copy

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CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213

CONTENTS

Introduction	4
Acknowledgments.....	7
Specimens Examined	10
Measurements and Symbols	11
Relative Age of Specimens	11
Comments	12
Systematic Account	12
Comparisons	12
Comparisons	16
External Appearance and Measurements	16
Sexual Dimorphism	20
External Nares	20
Rostrum	20
Infraorbital Foramen	21
Zygoma	22
Orbits	22
Size of Brain Case	23
Basicranial Flexure	23
Sinuses	23
Mandible	24
Size of Teeth and Diastemas	24
Cups and Cingula	25
Incisors	25
Canines	27
Discussion and Conclusions	33
References Cited	35

INTRODUCTION

A third species of living peccary (Fig. 1), *Tayassuidae*, representing a generic addition to the fauna of the Paraguayan Chaco, was announced by Wetzel, Dubos, Martin, and Myers (1975). We assigned this form to the genus *Catagonus* Ameghino, formerly known only from the Lower and Middle Pleistocene of Argentina, and indicated evidence of its close relationship to the genus *Platygonus* LeConte from the Upper Pliocene to postglacial times. We postulated that *Catagonus* occurs in most or all of the Gran Chaco. Since that writing, two skulls of *Catagonus*, collected in 1936 by José Yepes from the Argentine province of Salta, have been identified (Wetzel and Crespo, 1976) and conversations with hunters in the Bolivian Chaco indicate that *Catagonus* also occurs in that nation. [Also see Olrog et al (1976)]

The Gran Chaco extends from southeastern Bolivia through western Paraguay and into northwestern Argentina. It is an area of thorn steppe or thorn forest, often with dense and spiny undergrowth. In Paraguay, the Chaco covers an area two-thirds the size of California and is traversed by the Trans-Chaco highway that begins north of Asunción and runs northwesterly to the Bolivian border. Rainfall decreases from 1400 mm per year in the palm savannah of the Paraguay River valley to 400 mm per year along the western border of Paraguay, where grasses and bare sand occur between the more scattered trees and shrubs. The landscape is virtually flat, broken by extensive grass and palm swamps in areas of higher rainfall and by a few permanent and numerous intermittent streams (see Wetzel and Lovett, 1974; Short, 1975). Western Paraguay occupies three-fifths of the nation, but has only 4% of the population. Except for the Mennonite farming communities around Filadelfia, the Paraguayan Chaco contains large ranches, occasional small army posts, and much unused land. Several different derivations of the word *Chaco* have been postulated, but an appropriate one is that it comes from the Quechuan *chacu*, meaning an abundance of animal life (Weil et al., 1972). José de Acosta stated that *chaco* was a method of hunting by encirclement, and Garcilaso de la Vega used *chacu* to mean the annual ceremonial hunt of the Incas, in which encirclement was the method of capture (Barbara G. Beddall, pers. commun.).

Zoogeographical studies that mention the Chaco have been largely without benefit of recent studies of its mammalian fauna. The more recent continental analyses treat the Gran Chaco as follows: Hershkovitz (1972) grouped the Chaco with other adjacent faunal

areas as a Paraná-Paraguay Valley District, a transitional zone between the Brazilian and Patagonian Subregions. Fittkau (1969) placed the Chaco on the boundary between the Guiana-Brazilian and the Andean-Patagonian Regions, but fragmented it among three extensive zoogeographic provinces. Müller (1973:143-145), after considering the overlap of northern and southern faunas, found sufficient endemic animal species and subspecies to designate a separate Chaco Center. He grouped (p. 175) the Chaco with nonforest dispersal centers that he considered to have alternately expanded in arid periods and contracted during moist periods of the Quaternary. Other recent authors who have summarized the evidence for this ebb and flow of xeric vs. mesic habitats and their biota during Quaternary glacial-interglacial cycles include Eden (1974), Haffer (1974), Van der Hammen (1974), Short (1975), and Fairbridge (1976). Blair (1976) compared the anurans of the Sonoran of North America, the Chaco, and the Monte. The data he reviewed for the Chaco were restricted to Argentina, and his use of the term Chaco was much broader than the use in this paper. Solbrig (1976) wrote that Cabrera (1971) designated one of his three principal floral divisions of Neotropical South America as the Chaco Dominion, and one of its seven subdivisions as the Chaco Province. It is this latter use, except for restricting the eastern border of the Chaco to the Río Paraguay, that I follow here.

Prior to our report of the Chacoan peccary, *Catagonus* was restricted to two extinct species. Ameghino (1904) named the genus *Catagonus* when he described *C. metropolitanus*, based on a palate in two fragments, from Lower Pleistocene deposits in the city of Buenos Aires. In the same paper he described from the Middle Pleistocene of Buenos Aires *Listriodon bonaerensis*, based on isolated teeth, and this species was later moved to the genus *Catagonus* by Rusconi (1930).

LeConte (1848) described *Platygonus* from the North American Upper Pleistocene, and several species have been described from South American deposits. Among these, Rusconi (1930) described *Platygonus (Parachoerus) carlesi* from Middle Pleistocene deposits near the Río Dulce in Santiago del Estero, western Argentina. *Platygonus carlesi wagneri* Rusconi (ibid.) was reported in association with pre-Hispanic funeral urns, artifacts, and a large modern mammalian fauna from the vicinity of Melero in Santiago del Estero (Fig. 2). Rusconi (1948) later raised *wagneri* to the level of species. Both *P. carlesi*

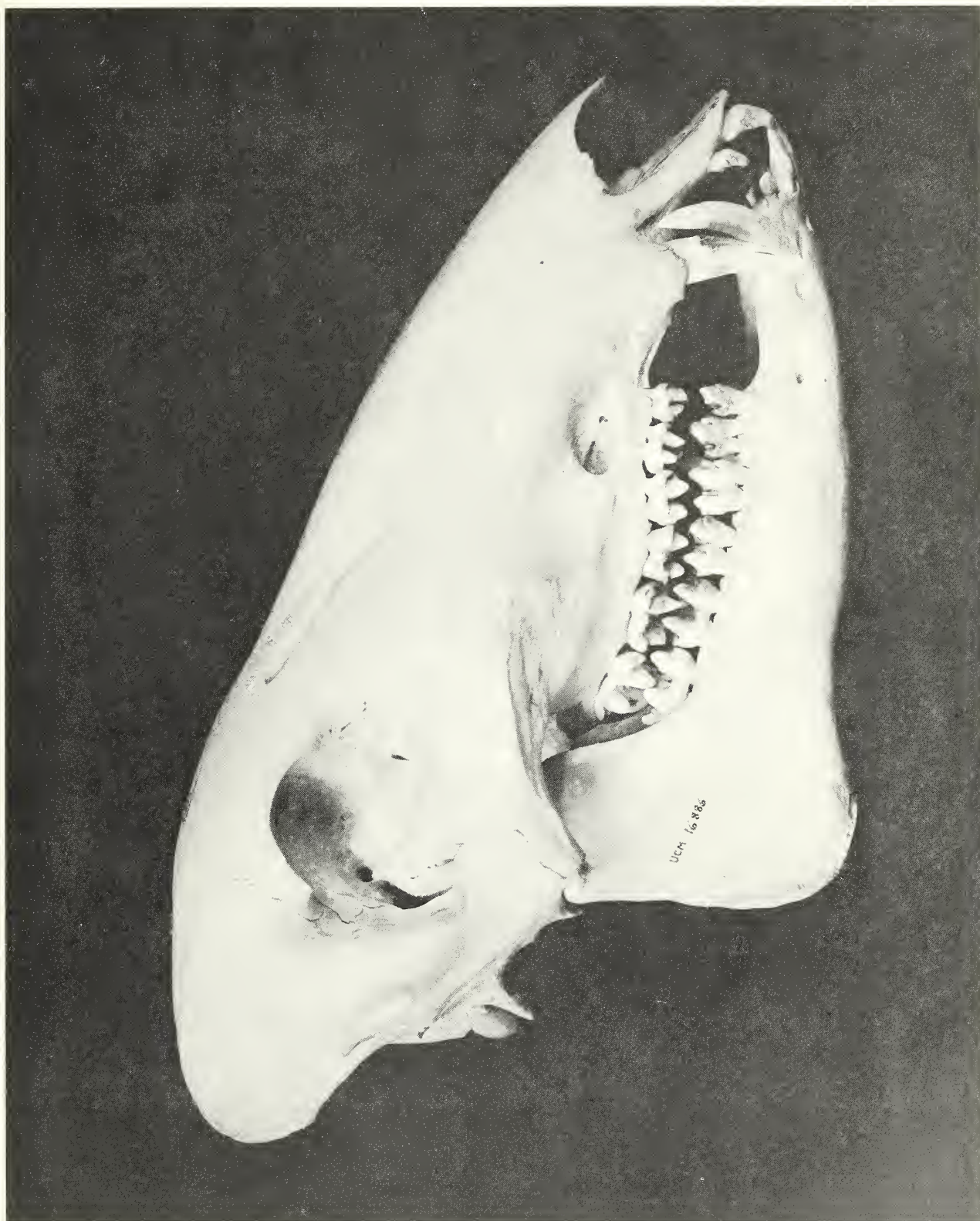


Fig. 1. Skull of the Chacoan peccary or Taguá, *Catagonus wagneri* (Rusconi). Specimen is CONN 16886, collected 10 km W Fortín Teniente Montaña, Depto. Boquerón, Paraguay, 21 July 1974.

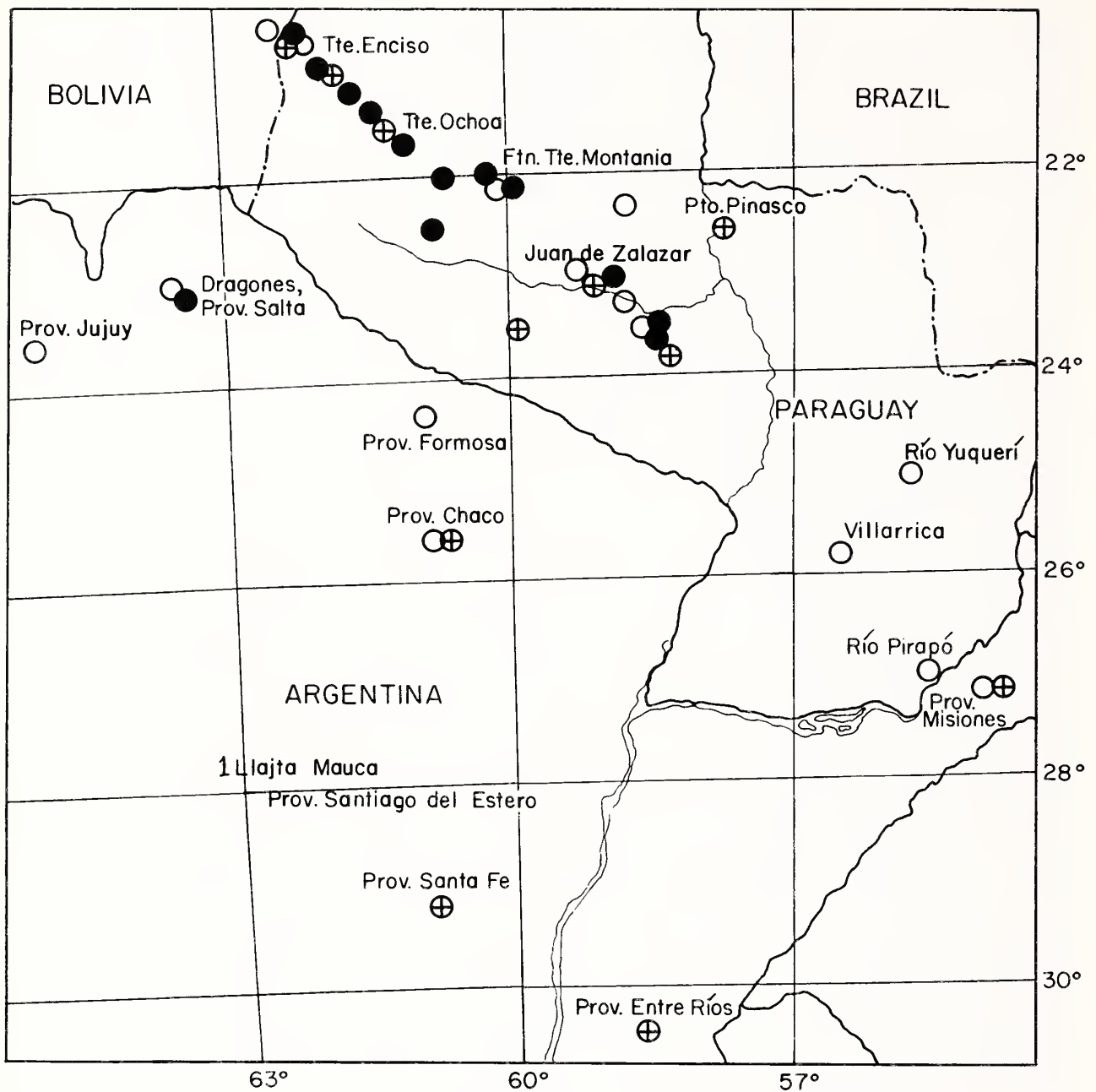


Fig. 2. Provenance of Recent peccary specimens examined. ● *Catagonus wagneri*. ⊕ *Tayassu pecari*. ○ *Tayassu tajacu*. 1, type-locality, *C. wagneri* (Rusconi 1930, 1948).

and *P. wagneri* were based upon complete or nearly complete crania.

The Chacoan peccary proved to be conspecific with *P. wagneri*. Despite the similarities of this species and *P. carlesi* to North American *Platygonus*, the molari-form premolars and larger molars were distinct from

all the *Platygonus* examined. *P. carlesi* and *P. wagneri*, in fact, were nearer to *Catagonus metropolitanus* and *C. bonaerensis* and were considered congeneric (Wetzel et al., 1975). I have since examined *Platygonus rebuffoi* Rusconi (1952), based upon a partial mandible, from the Middle Pleistocene of Uruguay

and find it assignable to the genus *Catagonus*. Thus all the species placed in the subgenus *Parachoerus* Rusconi belong, in my view, to the genus *Catagonus*.

In the Chaco, *Catagonus wagneri* is distinguished from the other living peccaries by any one of a number of Guaraní or Spanish names, e.g., Paguá, Taguá, or Curé-buro. The white-lipped peccary, *Tayassu pecari* (Link.), is there known as Tagnicate or Tâchycâtí, and the collared peccary, *T. tajacu* (L.), as Tayté-tou or Cure-í. The Recent specimens of *C. wagneri* are here described in more detail than was possible in the first brief report, and are contrasted with *T. pecari* and *T. tajacu* from Paraguay and adjacent Argentina. During the course of this study, such repeated comparisons have strongly emphasized the much closer relationship of *T. pecari* and *T. tajacu*. I am therefore abandoning Woodburne's (1968) generic separation into *T. pecari* and *Dicotyles tajacu*, and returning to a congeneric treatment of those two species. Detailed comparisons of the crania of *T. pecari* and *T. tajacu* may be found in both Rusconi (1929) and Woodburne (1968), and comparisons of those two species with *Platygonus compressus* in Guilday, Hamilton, and McCrady (1971). Such comparisons are therefore not repeated here. Comparisons with fossil forms are restricted to those assigned to the genera *Catagonus*, *Platygonus*, and, for comparative purposes, samples of *Prosthennops* Gidley and *Mylohyus* Cope. The genus *Selenogonus* Stirton (1947) from the Upper Pliocene or Pleistocene of Colombia is not included in the comparisons,

and I have avoided a definite stand on the genus *Argyrohyus* Kraglievich (1959) from the Upper Pliocene of Argentina. Neither holotype was examined, and the limited information in the descriptions, because of the fragmentary nature of the specimens, dictates restraint in commenting on those important specimens. I use *Platygonus marplatensis* Reig (1952), rather than *Argyrohyus chapadmalensis* (Castellanos) which Kraglievich considered the senior synonym. This is both a convenience and a bias on my part. In the use of *Platygonus chapadmalensis* (Ameghino) for another specimen (MMCN 246) in the collection at Mar del Plata, I have followed Reig.

In June 1975, during a visit to the Museo Argentina de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, the holotype of *C. bonaerensis* was photographed and measured. Unfortunately, the holotype of *C. metropolitanus* has been lost. Hereinafter, measurements of *C. metropolitanus* are from Rusconi (1930). Rusconi's holotypes of *C. wagneri* and *C. carlesi* have not as yet been located. Measurements in this paper, therefore, are from Rusconi (1930, 1948). Most measurements for *P. compressus* from Welsh Cave, Kentucky, are from Guilday et al. (1971). When my measurements of this species are given, the number of specimens is always indicated. Measurements of crania, teeth, and metapodials of *C. wagneri* from the Chaco of Paraguay are listed in Table 1 and may be compared with Rusconi's measurements of his holotypes and with Guilday's measurements of *P. compressus*.

ACKNOWLEDGMENTS

My wife, Drew S. Wetzel, has been continually involved in this study during most of the trips to examine specimens in museums and in preparation of this manuscript. Encouragement and sponsorship of our fieldwork in Paraguay, 1972-1975, have been generously provided in Asunción by Ing. Hernando Bertoni, Ministro de Agricultura y Ganadería, República del Paraguay; Ambassador George W. Landau and his staff of the Embassy of the United States; and Mr. Robert J. Eaton. Peter M. Berrie, ISCES, organized the fieldwork of 1972. Robert L. Martin participated in the fieldwork of 1973-1975; J. W. Lovett in 1972-1973; Juan Balbuena in 1972 and 1974; Philip Hazelton in 1973 and 1975. In 1975 Robert Dubos, John J. Mayer, Philip N. Brandt, and Juan Guerrero Cruz were also colleagues in the field. Philip

Myers collected three of the *C. wagneri* specimens. These are in the mvz, Berkeley, collection. Of numerous hunters interviewed in the Chaco, P. Erhard Schneider and Hans Enns of Filadelfia, Hugo and Jorge di Stilio of San Nicolas, Argentina, and Alberto and Oscar Arrigoni of Buenos Aires provided experienced observations on the habits and abundance of the three species of peccaries.

John E. Guilday, Malcolm C. McKenna, Clayton E. Ray, Duane A. Schlitter, Frank C. Whitmore, Jr., and Michael O. Woodburne provided encouragement and advice. Gerald E. Schultz made helpful comments on the Blancan. For advice on location of specimens of fossil tayassuids, thanks are due J. F. Bonaparte, Guillermo del Corro, Paul S. Martin, Larry G. Marshall, Alvaro Mones, and Rosendo Pascual.

Table 1. Skeletal measurements, *Catagonus wagneri*, Chaco of Paraguay.

Measurement	\bar{Y}	s	C	O.R.	N
Crania with adult dentition					
Greatest length	309.9	6.7	2.2	298-324	29
Condylbasal length (CBL)	266.6	7.2	2.7	252-280	27
Basal length	255.7	7.4	2.9	241-268	26
Anterior border of orbit to anterior of premaxilla (RL)	199.1	5.2	2.6	191-209	31
Postrostral length (CBL-RL adj. = PRL)	71.4	4.1	5.8	62.6-77.0	27
Anterior border of orbit to margin of infraorbital foramen	86.7	3.6	4.1	81.1-97.4	31
Zygomatic breadth	125.6	5.7	4.5	108-137	25
Depth of suborbital zygoma	30.3	2.3	7.6	26.0-35.2	30
Depth of zygoma: postorbital process of zygoma to pregenoid process	56.0	2.7	4.8	50.9-61.0	24
Vertical diameter of orbit	35.8	1.0	2.8	33.4-37.7	31
Width across canines	60.5	2.4	4.0	55.8-65.7	28
Width across canine buttresses	64.3	2.4	3.8	60.5-69.2	27
Width, maximal, across molar rows	64.4	3.0	4.7	59.0-74.0	27
Width, minimal, between P ² 's	27.2	2.0	7.2	22.7-32.4	29
Width, minimal, between M ² 's	24.7	1.9	7.6	20.8-29.9	30
Width, minimal, between orbits	77.5	4.1	5.3	70.0-89.0	30
Width across postorbital processes	100.4	3.9	3.9	93-109	29
Length of precanine diastema	20.1	2.3	11.6	13.3-26.3	31
Length of postcanine diastema	23.9	3.2	13.4	18.8-29.1	31
Height of nasal opening	31.2	1.2	3.8	29.0-33.3	23
Height of occiput from ventral border of condyles	100.4	4.2	4.2	93-109	26
Width across occipital condyles	43.6	1.6	3.5	40.1-46.1	26
Cranial capacity	114.1	7.9	6.9	102-130	22
Mandibles with adult dentition					
Length, condyle to tip	209.8	5.7	2.7	200-222	20
Height, maximal, posterior	93.0	3.5	3.7	86-99	20
Width, maximal, posterior	109.8	7.2	6.6	99-122	21
Length of postcanine diastema	30.8	4.1	13.4	21.4-36.4	23
Depth below middle of postcanine diastema	23.4	1.4	6.0	20.2-25.3	23
Depth below anterior margin of M ₁	31.2	1.8	5.8	25.8-33.6	23
Length of symphysis	56.2	3.2	5.7	47.4-61.8	21
Deciduous dentition					
dP ²⁻⁴ , length	33.3	---	---	---	1
dP ² , length	9.2	---	---	---	1
width	7.5	---	---	---	1
dP ³ , length	11.6	---	---	11.1, 12.2	2
width	11.2	---	---	10.3, 12.2	2
dP ⁴ , length	13.3	---	---	13.1-13.7	3
width	12.4	---	---	12.1-12.7	3
dP ²⁻⁴ , length	34.8	---	---	34.1-35.3	4
dP ² , length	7.4	---	---	6.7-7.8	4
width	4.0	---	---	3.9-4.0	5
dP ³ , length	9.8	---	---	9.6-10.2	5
width	6.4	---	---	6.1-6.6	5
dP ⁴ , length	18.2	---	---	17.7-18.9	5
width	10.4	---	---	10.2-10.5	5

Table 1. Skeletal measurements, *Catagonus wagneri*, Chaco of Paraguay (continued).

Measurement	\bar{Y}	s	C	O.R.	N
Permanent dentition					
P ² -M ³ , length	94.8	2.6	2.7	91.0-99.1	23
P ² -4, length	38.2	1.9	5.0	32.1-41.3	26
M ¹ -3, length	57.9	2.5	4.4	52.7-64.9	27
Upper canine, anteroposterior diameter	15.1	1.0	6.5	13.5-17.3	24
transverse diameter	10.4	0.8	7.7	9.0-12.2	23
P ² , length	11.4	0.6	5.6	10.1-12.8	29
width	9.6	0.7	7.1	8.4-11.1	29
P ³ , length	13.2	0.8	6.0	11.5-14.8	34
width	13.1	0.7	5.2	12.1-14.6	33
P ⁴ , length	15.0	0.8	5.6	13.1-17.8	36
width	15.2	0.8	5.3	13.6-16.9	36
M ¹ , length	16.6	1.0	5.9	14.7-18.4	38
width	15.4	0.7	4.5	14.0-16.9	37
M ² , length	20.6	0.9	4.5	18.7-22.5	37
width	18.8	1.0	5.1	17.0-20.9	37
M ³ , length	22.3	1.3	5.9	20.1-25.4	28
width of anterior moiety	18.9	1.0	5.3	16.5-20.6	27
width of posterior moiety	17.4	0.8	4.3	16.1-18.6	28
P ₂ -M ₃ , length	98.7	3.8	3.8	90.5-107.6	16
P ₂ -4, length	37.4	2.0	5.4	32.8-41.5	16
M ₁ -3, length	61.9	2.0	3.2	58.0-66.7	21
Lower canine, anteroposterior diameter	15.4	0.9	5.7	13.7-17.0	18
transverse diameter	10.5	0.7	6.8	9.0-11.7	18
P ₂ , length	9.3	0.6	6.4	7.8-10.1	15
width	5.9	0.5	7.7	5.4-6.8	15
P ₃ , length	12.6	0.6	5.1	11.3-14.0	19
width	8.8	0.5	5.4	8.1-9.8	19
P ₄ , length	16.2	1.0	6.2	14.4-19.4	22
width	12.6	0.6	5.1	11.4-13.8	22
M ₁ , length	17.0	0.9	5.4	15.2-18.8	28
width	13.0	0.5	3.9	11.9-13.9	28
M ₂ , length	20.5	1.0	4.7	18.7-22.3	28
width	16.5	0.6	3.8	15.1-17.8	27
M ₃ , length	26.2	1.6	6.0	24.3-30.6	21
width of anterior moiety	16.4	0.8	5.1	14.9-18.1	21
width of posterior moiety	15.9	0.6	3.8	14.4-16.8	21
Length of metapodials					
Metacarpal II	41.5			39.8-44.4	4
III	67.4			65.1-70.5	5
IV	69.8			68.5-71.4	5
V	52.6			50.3-53.7	5
Metatarsal II	47.2			43.6-51.2	4
III	80.0			79.0-81.5	5
IV	82.4			81.5-83.4	5
V	48.6			46.0-50.4	5

At this University, Robert E. Dubos measured many of the skulls with me, John J. Mayer noted the similarity to *Platygonus*, Theodore A. Heist adapted data for computer analysis, Mary Hubbard and her staff prepared the figures, Adelaide Ellsworth and Robert Pirozok sectioned hairs, and Solomon E. Wollman photographed the skull and toothrows.

I am especially indebted to the following institutions and curators who generously permitted examination of specimens under their care. The following abbreviations are used in later accounts to identify the location of specimens:

AMNH—The American Museum of Natural History, New York, Malcolm C. McKenna.

BMNH—British Museum (Natural History), London, G. B. Corbet.

CM—Carnegie Museum of Natural History, Pittsburgh, Mary R. Dawson.

CONN—The University of Connecticut Museum of Natural History, Storrs.

MACN—Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Guillermo del Corro and Jorge A. Crespo.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Barbara Lawrence.

MDC—Museo Departmental de Colonia, Uruguay, Bautista Rebuffo.

MHN—Museo de Historia Natural, Universidade Federal de Minas Gerais, Belo Horizonte, José Silvio Fonseca.

MMCN—Museo Municipal de Ciencias Naturales, Mar del Plata, Galileo J. Scaglia.

MN—Museu Nacional, Rio de Janeiro, Fernando D. de Avila-Pires and Fausto L. de Souza Cunha.

MNHN—Museo Nacional de Historia Natural, Montevideo, Alvaro Mones and Alfredo Ximénez.

MU¹—The Museum, Texas Tech University, Lubbock, Patricia Vickers Rich.

MVZ—Museum of Vertebrate Zoology, University of California, Berkeley, J. L. Patton.

TMM—Texas Memorial Museum, University of Texas, Austin, Ernest L. Lundelius, Jr.

USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C., Charles O. Handley, Jr. and Clayton E. Ray.

Support for this study was provided by the National Geographic Society from 1973 through 1975. Additional funds were supplied by the University of Connecticut Research Foundation in 1973 and the Carnegie Museum of Natural History in 1975.

SPECIMENS EXAMINED

Collection sites along the Trans-Chaco highway of Paraguay are given in kilometers (Km) from the beginning of the road at Villa Hayes, northeast of Asunción. Lower case (km) is used for distances from other points. Numbers preceding abbreviations for museums indicate the number of specimens examined. Numbers following such abbreviations are museum accession numbers.

Catagonus wagneri, Recent—56 (Fig. 2). ARGENTINA. Salta: 1 MACN, unspecified locality; 1 MACN, Dragones. PARAGUAY. Boquerón: 4 CONN, 28-40 km N Filadelfia, road to Fortín Teniente Montaña; 5 CONN, 10-42 km W Ftn. Tte. Montaña, road to Mariscal Estigarribia; 1 CONN, Km 480; 1 CONN, Km 530; 1 CONN, Ftn. Capitán O. Serebriakof. Nueva Asunción: 12 CONN, Km 555-607, vicinity of Tte. Ochoa; 24 CONN, Km 613-667, vicinity of Tte. Enciso; 2 CONN, Km 764, Ftn. Sgto. Rodríguez (Villazón). Presidente Hayes: 3 MVZ, Km 275; 1 CONN, Km 277.

Catagonus spp., fossil. ARGENTINA. Buenos Aires: MMCN 41, NNE Mar del Plata (Miramar Form., Ensenadense, Mid-Pleistocene); MMCN 707, Ciudad de San Antonio de

Areco ("Bonaerense?," Mid-Pleistocene?); MMCN 972, Ayo. Lobería (Barranca Lobos Form., inf., Lower Pleistocene). Distrito Federal: MACN 2440, *L. bonaerensis* Ameghino, holotype (Bonaerense, Mid-Pleistocene). URUGUAY. Colonia: MDC 1345, *P. rebuffoi* Rusconi, holotype, 50 km N Colonia del Sacramento (Bonaerense, Mid-Pleistocene).

Platygonus spp. ARGENTINA. Buenos Aires: MMCN 25, *P. marplatensis* Reig, holotype, Barranca de Los Lobos, 1 km NE Baliza Caniú (layer 3, Chapadmalal Form., Montehermosense, Upper Pliocene); MMCN 156, *P. scagliae* Reig, holotype, Chapadmalal (Barranca de Los Lobos Form., Vorhué inf., Uquiense, Lower Pleistocene); MMCN 246, Punta San Andrés (Vorhué inf., Uquiense, Lower Pleistocene); MMCN 878, SW Ayo. Lobería (Barranca de Los Lobos Form., Uquiense, Lower Pleistocene); MMCN 1212, Cañada Chapar (Vorhué inf., Lower Pleistocene). BRAZIL. Minas Gerais: 3 MHN, caves (Pleistocene-subRecent). MEXICO. Guanajuato: 1 USNM, *P. alemanii* Dugès, holotype, Moroleón (Pleistocene). UNITED STATES. Arizona: 4 AMNH, Papago Springs (Rancholabrean). Florida: 1 USNM, Melbourne (Pleistocene). Idaho: 1 USNM, Hagerman Form. (Hemphillian). Kansas: 9 AMNH, Edson Quarry (Hemphillian). Kentucky: 15 CM, Welsh Cave (Rancholabrean). Maryland: 8 USNM, *P. cum-*

¹The symbol TTU-P was inadvertently not used to indicate the paleontological collection of The Museum, Texas Tech University.

berlandensis Gidley, incl. holotype, Cumberland Cave (Irvingtonian). Missouri: 7 AMNH, Cherokee Cave (Rancholabrean). Nebraska: 1 AMNH, Snake Creek Form. (Hemphillian). Tennessee: 5 CM, Guy Wilson Cave (Rancholabrean). Texas: 2 MU, Carter Quarry (Blancan); 3 TMM, Crosby Co. (Blancan); 1 AMNH, Channing area ("Hemphillian-Blancan").

Prosthennops spp. UNITED STATES. California: 1 AMNH, Eden (late Hemphillian). Florida: 1 AMNH, Mixon Bone Bed (late Hemphillian). Nebraska: 1 AMNH, Snake River (Valentinian, Lower Pliocene); 3 AMNH, Ash Hollow Form. (late Clarendonian, Lower Pliocene). URUGUAY. Colonia: MDC 398, ?*Prosthennops uruguayensis* Rusconi, holotype, 12 km N Colonia del Sacramento (Pampean Form., Belgranense, Mid-Pleistocene).

Mylohyus spp. UNITED STATES. Arkansas: 1 AMNH, Conard Fissure (Irvingtonian). Florida: 1 AMNH, Seminole Field (Rancholabrean).

Tayassu pecari, Recent—37 (Fig. 2). ARGENTINA. Chaco: 2 MACN, unspecified locality. Entre Ríos: 1 BMNH, unspecified locality. Misiones: 3 MACN, unspecified locality.

Santa Fe: 1 MACN, unspecified locality. PARAGUAY. 1 MNHN, unspecified locality. Nueva Asunción: 3 CONN, Tte. Enciso; 1 CONN, Garrapatel-í, 7 km SW Km 620; 1 CONN, Km 592; 6 CONN, Ftn. Sgto. Rodríguez. Presidente Hayes: 13 CONN, Juan de Zalazar; 1 CONN, Km 194; 1 MVZ, Km 275; 2 USNM, Pto. Pinasco; 1 CONN, 85 km W Pozo Colorado, 10 km N road to Ftn. Ávalos Sánchez.

Tayassu tajacu, Recent—59 (Fig. 2). ARGENTINA. Chaco: 1 MACN, unspecified locality. Formosa: 1 MACN, unspecified locality. Jujuy: 1 BMNH, 1 MACN, unspecified localities. Misiones: 5 MACN, unspecified localities. Salta: 16 MACN, Dragones; 1 MACN, Urundel. BOLIVIA. Chuquisaca: 1 CONN, 8 km E Santa Rosa. PARAGUAY. Boquerón: 4 CONN, 29 km N Filadelfia, road to Ftn. Tte. Montania. Caaguazú: 2 MCZ, Río Yuquerí. Guairá: 2 BMNH, Villarrica. Itapúa: 1 CONN, Pto. Pirapó. Nueva Asunción: 1 CONN, Km 750, Ftn. Gral. E. A. Garay; 5 CONN, Km 764, Ftn. Sgto. Rodríguez; 1 CONN, Km 607; 3 CONN, Tte. Enciso. Presidente Hayes: 3 CONN, Estancia-í, 100 km E Filadelfia; 7 CONN, Juan de Zalazar; 3 MVZ, Km 275.

MEASUREMENTS AND SYMBOLS

All linear measurements, given in millimeters, were taken with dial calipers accurate to .1 and, for the larger dimensions, with GPM calipers accurate to 1. The cranial measurements used in Table 1 and elsewhere include most of those used by Guilday et al. (1971) and Rusconi (1930, 1948) plus the following additions and derivations:

Height of nasal opening: Distance from the most anterior point of nasal bone to midline of dorsal surface of premaxilla, in a line at right angles to the toothrow.

Cranial capacity: An estimate, given in milliliters, of the volume of brain cavity, based upon volume of small beans required to fill the cavity.

Rostral length (RL): Distance from anterior tip of premaxilla to anterior margin of orbit.

Rostral length, adjusted (RL adj.): Distance from

anterior tip of premaxilla, along midline axis of skull, to a line between the anterior margins of orbits. RL adj. is derived as the altitude of a triangle in which RL is the hypotenuse and one-half the interorbital width is the base.

Postrostral length (PRL): Distance from anterior margin of orbits, along the midline axis, to a line across the posterior margin of occipital condyles. PRL is derived as the difference between condylo-basal length and RL adj.

Symbols used in the Tables and elsewhere refer to: \bar{Y} = mean or \bar{X} ; s = standard deviation of the sample (S.D. of Simpson, 1949 and Guilday et al., 1971); C = coefficient of variation computed as s/\bar{Y} (V of Simpson and of Guilday); O.R. = observed range; N = number in sample.

RELATIVE AGE OF SPECIMENS

Following Herring's (1974) method, I rated the degree of closure of 22 cranial sutures for 45 *C. wagneri*, 21 *T. pecari*, and 20 *T. tajacu*, all CONN specimens from Paraguay. The relative sequence of closure of these sutures within each species was then compared by mean suture fusion scores and by plotting suture closure against age categories. Arbitrary age categories

were based upon the following chronology of tooth eruption and wear. These age categories were applied to all three species, but the following sequence of suture closure is for *C. wagneri*.

0. Immature: Only deciduous teeth in place; no molars present.

1. Young juvenile: Deciduous premolars and first

molar in place. Sutures closed by end of period: interparietal and occipito-parietal.

2. Juvenile: Deciduous premolars and first two molars in place. Sutures closed by end of period: interfrontal and intermaxillary; sutures beginning to close: naso-frontal and occipitals.

3. Young adult: Permanent premolars and first two molars in place. Additional sutures closed by end of period: basispheno-occipital, naso-frontal, and occipitals; sutures beginning to close: fronto-parietal, internasal, interpremaxillary, jugo-frontal, maxillo-frontal, maxillo-jugal, naso-maxillary, occipito-squamosal, premaxillo-maxillary, premaxillo-nasal.

4. Adult: Third molar in place, but without wear. Additional sutures closed by end of period: fronto-parietal, internasal, interpremaxillary, jugo-frontal, maxillo-frontal, maxillo-jugal, naso-maxillary, occipito-squamosal, premaxillo-maxillary; sutures beginning to close: alispheno-squamosal, basispheno-presphenoid, jugo-squamosal, maxillo-alisphenoid, parieto-squamosal.

5. Adult: Moderate wear on first and second molars, slight wear on third molar. Additional sutures closed by end of period: alispheno-squamosal, jugo-squamosal, maxillo-alisphenoid, parieto-squamosal, premaxillo-nasal.

6. Adult: Moderate to heavy wear on first two molars, moderate wear on last molar. Additional suture closed before end of period: basispheno-presphenoid.

7. Old adult: Molars worn to basins.

COMMENTS: The sequence of eruption of premolars and molars proved to be the same in all three species. The age at which teeth erupted is not known for *C. wagneri* nor *T. pecari*. Kirkpatrick and Sows

(1962) determined the sequence and time of tooth eruption in 26 captive *T. tajacu* in Arizona. In that species the first two upper molars were present by 43 (37-50) weeks of age, the permanent upper premolars by 72 (66-83) weeks, and the last upper molars by 83 (74-94) weeks; there was no significant difference between upper and lower dentition.

The relative sequence of closure of cranial sutures is indicated in Table 2 for the three peccaries as mean suture fusion scores and as the sequence of closures within each species. As the samples for this comparison are restricted to CONN specimens from Paraguay and all but one specimen, *T. tajacu* from southeastern Paraguay, are from the Chaco, any possible effect of geographical variation upon sequence of closure has been reduced. This geographical homogeneity and some dissimilarity in sutures chosen for scoring may explain variation between the differences found by Herring (1974) for the species of *Tayassu* and the differences found in my study. The major differences found here, however, are between *C. wagneri* on one hand and the two species of *Tayassu* on the other. Of 22 sutures rated, 18 differed from *Tayassu* by more than .1 fusion score and one closure rank or more. Seven of the 22 sutures closed earlier and 10 sutures closed later than in *T. pecari* and *T. tajacu*. Fusion scores for internasal and basispheno-presphenoid sutures differed from the other species by more than .2 but fell between the scores of the two *Tayassu*. For the remaining three sutures scored, the fusion score in *C. wagneri* was similar to *T. tajacu* for occipito-parietal and similar to *T. pecari* for interpremaxillary and basispheno-occipital.

SYSTEMATIC ACCOUNT

Catagonus Ameghino

Catagonus Ameghino, 1904:188; Rusconi, 1930:164; Wetzel et al., 1975.

TYPE SPECIES: *C. metropolitanus* Ameghino, loc. cit. Holotype not at MACN, June 1975. Ensenadense, Mid-Pleistocene, Argentina, Buenos Aires.

Listriodon bonaerensis Ameghino, 1904:186. Holotype: MACN 2440. Bonaerense, Mid-Pleistocene, Argentina, Buenos Aires.

Platygonus (Parachoerus) carlesi Rusconi, 1930:150. Holotype not at MACN, June 1975. Bonaerense, Mid-Pleistocene, Argentina, Santiago del Estero, Las Termas, Río Dulce.

Catagonus (Interchoerus) bonaerensis.—Rusconi, 1930:168, based upon Ameghino, 1904:186.

Platygonus (Parachoerus) carlesi wagneri Rusconi, 1930:231 and *Platygonus wagneri*.—Rusconi, 1948:231. Pre-Hispanic deposits, Argentina, Santiago del Estero, Lajta Mauea.

Platygonus (Parachoerus) rebuffoi Rusconi, 1952:125; Mones and Francis, 1973:77. Holotype: MDC 1345. Bonaerense, Mid-Pleistocene, Uruguay, Colonia, Arroyo de Las Limetas. RANGE OF CATAGONUS: Lower Pleistocene of Argentina and Uruguay to Recent of Gran Chaco.

COMPARISONS: The skull of *Catagonus* (Fig. 1) is similar to *Platygonus* and differs from *Tayassu* (including *Dicotyles*) in having extreme development of the rostrum, nasal chamber, and sinuses; braincase

proportionally and often actually smaller; infraorbital foramen well anterior to zygomatic arch; pronounced articular fossa absent on anterior face of zygomatic arch; zygomatic bar below orbit deeper; orbits more posterior in position, anterior edge of orbit well posterior to last molar, and postorbital process of zygomatic well posterior to pregenoid process; pronounced basicranial flexure; teeth hypsodont; and molars with four major cusps.

Cranial characters of *Catagonus* that distinguish it from *Platygonus* (Fig. 3) are: molars larger, toothrows longer; postcanine diastemas shorter; premolars and molars with cuspules; last premolars (P^4 molariform, with four major cusps vs. two cusps; cingula well developed on most premolars and molars, complete on buccal side of all upper premolars and molars; lower first premolar (P_2) with a single major cusp (Fig. 4) vs. paired lateral cusps; last upper molar (M^3) quadrangular, lacking a pronounced posterior constriction in transverse width. Excepting the earliest forms of *Platygonus*, *Catagonus* also differs in having three pairs of lower incisors and a more gracile skull that lacks the flared zygomata and keeled genium.

Catagonus is similar to *Prosthennops* in that the last premolars are molariform, but differs from the latter in having larger molars with cingula more completely developed, longer toothrows, and shorter postcanine diastemas. A more definitive separation of *Prosthennops* (with the latest occurrence in the Upper Pliocene) from *Catagonus*, which was first known from the Lower Pleistocene, awaits a better understanding of the upper limits of *Prosthennops*.

Catagonus differs from *Platygonus* (*Brasiliochoerus* Rusconi, 1930) in having the M^3 larger than M^2 , particularly for the anteroposterior diameter. *Brasiliochoerus* is unusual among the Pliocene-to-Recent tayassuids of North and South America in having the M^3 smaller than M^2 for both anteroposterior and transverse diameters, as shown in Table 3. The remaining characters presented by Rusconi are not unique to *Brasiliochoerus*: (1) The features of molariform premolars and the P^1 with four main cusps and nearly the same size as M^1 are shared by *Catagonus*, *Brasiliochoerus*, *Prosthennops* and *Mylohyus*. (2) A glenoid fossa ventral to the orbit and, although not listed by Rusconi, an anterior opening of the infra-

Table 2. Comparison of mean suture fusion scores* and sequence of closure of cranial sutures for the three species of Recent peccaries. Suture fusion scoring follows Herring (1974): 0 = unfused, 1 = less than half fused, 2 = about half fused, 3 = more than half fused, and 4 = completely fused.

Cranial suture	<i>C. wagneri</i>		<i>T. pecari</i>		<i>T. tajacu</i>	
interparietal	3.98	1st	3.46	2nd	3.40	2nd
occipito-parietal	3.95	2nd	3.63	1st	3.92	1st
interfrontal	3.89	3rd	3.46	2nd	3.40	2nd
occipitals	3.82	4th	3.39	7th	3.23	5th
intermaxillary	3.64	5th	3.46	2nd	3.40	2nd
naso-frontal	3.58	6th	3.46	2nd	3.22	6th
occipito-squamosal	3.50	7th	1.72	21st	2.28	17th
premaxillo-maxillary	3.16	8th	3.46	2nd	3.22	6th
internasal	3.11	9th	3.37	8th	2.93	14th
interpremaxillary	3.07	10th	3.04	14th	2.86	15th
naso-maxillary	2.98	11th	3.24	9th	3.22	6th
fronto-parietal	2.96	12th	2.83	15th	2.79	16th
basispheno-occipital	2.85	13th	2.80	16th	3.12	11th
premaxillo-nasal	2.80	14th	3.24	9th	3.08	12th
maxillo-frontal	2.78	15th	3.12	11th	3.22	6th
jugo-frontal	2.73	16th	3.07	13th	3.03	13th
maxillo-jugal	2.49	17th	3.16	11th	3.17	10th
maxillo-alisphenoid	1.86	18th	2.33	18th	2.18	19th
alispheno-squamosal	1.67	19th	1.82	20th	1.90	21st
jugo-squamosal	1.62	20th	1.95	19th	2.22	18th
basispheno-presphenoid	1.62	20th	1.16	22nd	1.99	20th
parieto-squamosal	1.58	21st	2.50	17th	1.90	21st

*Original mean suture fusion scores for entire samples: *C. wagneri*, 2.893; *T. pecari*, 3.188; *T. tajacu*, 2.915. The following constants were applied to adjust *Tayassu* samples to a mean age equivalent to that of *Catagonus* sample: *T. pecari*, .9075; *T. tajacu*, .9923.

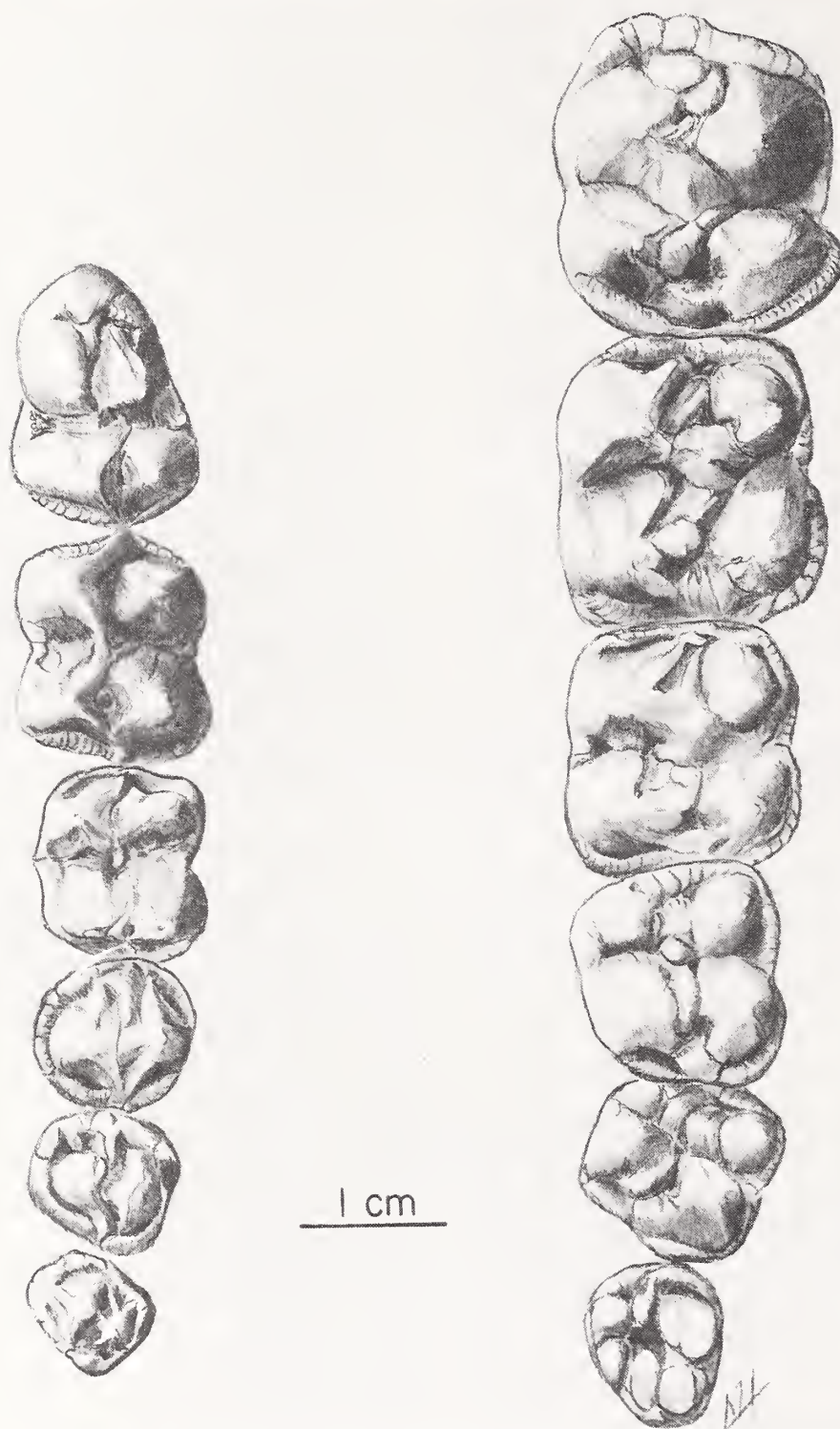


Fig. 3. Right maxillary toothrows, P²-M³. Left, *Platygonus compressus*, CM 20114, Welsh Cave, Kentucky. Right, *Catagonus wagneri*, CONN 16886, Chaco of Paraguay. Artist, Mary M. Hubbard.

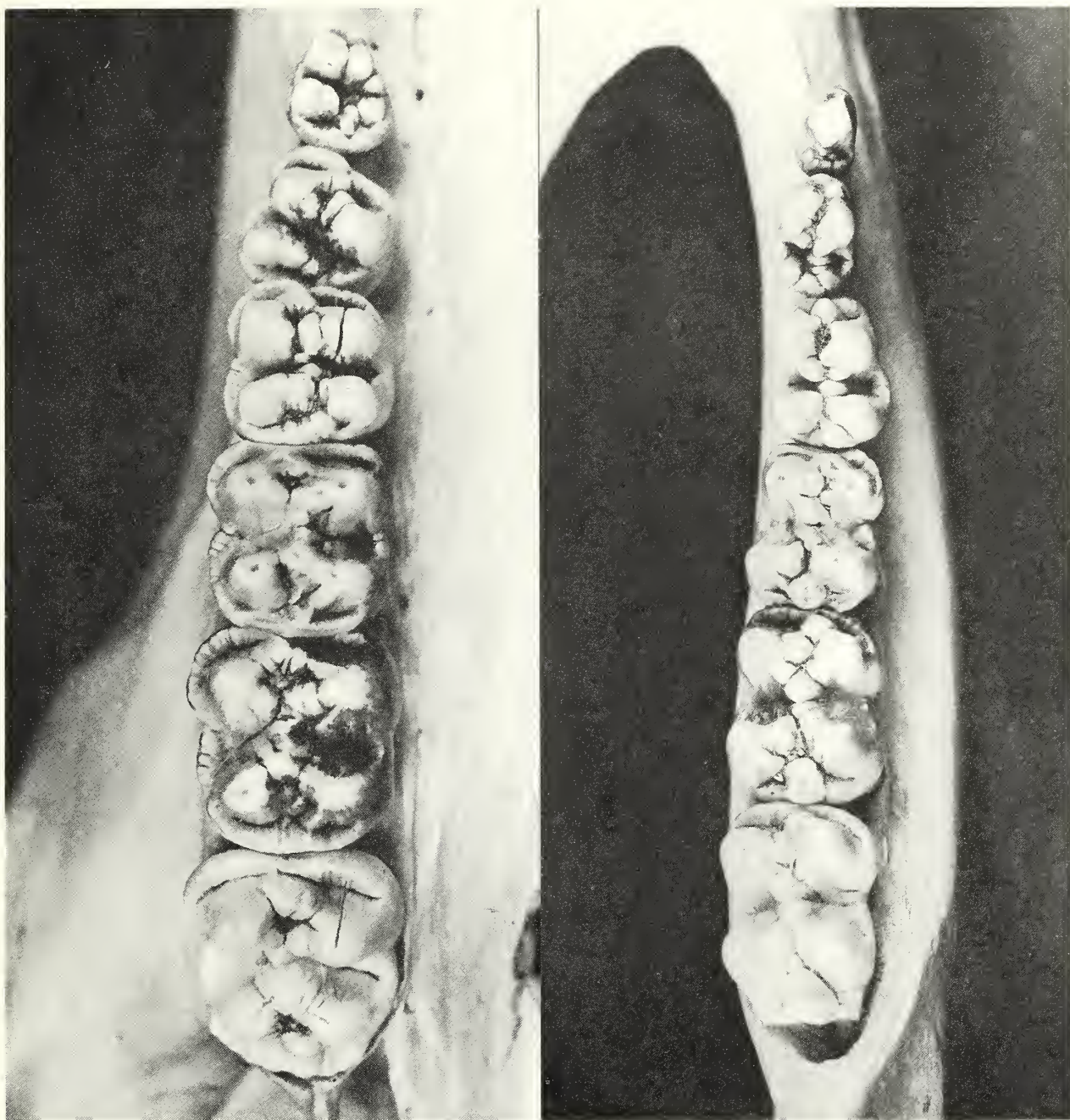


Fig. 4. Right cheek teeth, *C. wagneri*, CONN 16886. Left, maxillary P^2 - M^3 . Right, mandibular P_2 - M_3 .

Table 3. Anteroposterior and transverse diameters of M^2 and M^3 for *Brasiliochoerus* and *Catagonus*. Except where stated otherwise, measurements are from Rusconi (1930).

	M^2	M^3
<i>Platygonus (Brasiliochoerus) platensis</i>	16.3/15.5	15.5/13.5
<i>P. (Brasiliochoerus) platensis parodii</i>	17.3/16	16 /14.3
<i>P. (Brasiliochoerus) stenocephalus</i> , Reinhardt (1880:295)	18 /18	17 /16
<i>P. (Brasiliochoerus) stenocephalus</i> ?*, Ameghino (1889:575)	16 /16	16 /13
<i>Catagonus bonaerensis</i>	19.6/18	22 /18
<i>C. carlesi</i>	19.8/18.5	22 /20
<i>C. wagneri</i> , \bar{Y} , holotype and paratype, Rusconi (1948:235)	19.6/19.5	21.5/19.5
<i>C. wagneri</i> , Recent of Paraguay, this study	20.6/18.8	22.3/18.9

*Considered by Rusconi (1930:176, 219) to be "*Catagonus (Interchoerus)*?"

orbital foramen near the middle of the rostrum occur in *Catagonus*, *Mylohyus*, *Prosthennops*, *Brasiliochoerus*, and most of the remaining species of *Platygonus*. These two characters are in contrast to *Tayassu* where the glenoid fossa is posterior to the orbit and the infraorbital foramen lies in the posterior third of the rostrum. Partial exceptions, discussed later, occur in those South American *Platygonus* that also display other features suggesting some proximity to the ancestry of *Tayassu*. (3) Slender, gracile skulls occur in *Catagonus*, *Brasiliochoerus*, and some early *Platygonus* as opposed to the more massive skulls with flaring zygomata and angular processes and large canine buttresses of most *Platygonus* and *Prosthennops*. (4) Long tooththrows and short diastemas occur in both *Catagonus* and *Brasiliochoerus*. The general similarity of *Catagonus* and *Brasiliochoerus* may be seen by comparing *C. carlesi* in Rusconi (1930: Plates 3, 4, 5) for the former genus with *P. stenocephalus* in Reinhardt (1880: Plate 7) and Winge (1906: Plate 6) for the latter subgenus. Only the M^2 vs. M^3 differences noted above and the larger premolars and molars of *C. carlesi* appear to separate the two taxa. If *Platygonus* is restricted by non-molariform premolars, *Brasiliochoerus* must be removed from the genus as Woodburne (1968:32) believed should be done eventually. The question then remaining would be the use of *Brasiliochoerus* as a genus, or as a subgenus of *Catagonus*, a question that cannot be resolved here.

Catagonus wagneri (Rusconi)

Platygonus carlesi wagneri Rusconi, 1930:231.

Platygonus wagneri.—Rusconi, 1948:231.

Catagonus wagneri.—Wetzel, Dubos, Martin, and Myers, 1975:379; Wetzel and Crespo, 1976:25.

TYPE-LOCALITY: Pre-Hispanic deposits, Argentina, Santiago del Estero, Lajta Mauca, 28°12'S, 63°05'W (Fig. 2).

RECENT RANGE AND HABITAT: Semiarid thorn-forest and steppe of the Gran Chaco; specimens reported in this study (Fig. 2) are from the middle to western Chaco of Paraguay and the province of Salta, Argentina. Interviews with hunters indicate that the present range extends into the Chaco of Bolivia and the Argentine provinces of Formosa, Chaco, and northern Santiago del Estero. Olrog, Ojeda, and Barquez (1976) report specimens from Nueva Esperanza, Depto. Pellegrini, in the latter province, as well as information on the tagua in the Chaco of Salta.

COMPARISONS

EXTERNAL APPEARANCE AND MEASUREMENTS:

Compared with the gray color of *T. tajacu* and the black of *T. pecari*, *C. wagneri* is a large brownish-gray peccary with a faint collar of lighter hairs across the shoulders. Hair on ears and legs is longer and paler in color than in *Tayassu*. The head is larger, and ears, legs, and tail are longer. The larger ear accounts, no doubt, for one of the local names, Curé-buro. Like *T. pecari* and *T. tajacu*, *C. wagneri* has vestigial hooves or dew claws on the reduced second and fifth digits of the forefeet. A single, median dewclaw is present on the posterior side of the hindfeet of *T. pecari* and *T. tajacu* but absent in *C. wagneri*. Dew claws are missing altogether in the extinct *P. compressus* and *P. cumberlandensis* (Guilday et al., 1971:291).

Mean measurements of five freshly killed adults and one young adult *C. wagneri* from the vicinity of Teniente Ochoa and Tte. Enciso in the western Chaco of Paraguay are as follows: Length of head + body, 1026 (♂♂ 1112, 923; ♀♀ 1005, 1005, 1087); length of tail, 86.7 (♂ . . . , 102; ♀♀ 88, 70, . . .); length of hindfoot to tip of longest hoof, 227.6 (♂♂

222, 235; ♀ ♀ 228, 238, 215); height of ear from notch, 119.4 (♂ ♂ 115, 118; ♀ ♀ 120, 120, 124); weight, one ♀, 37 kg.

Although most of our Paraguayan specimens of the three species of peccaries are skulls from hunters' kills, the external measurements of *C. wagneri* may be compared with the following means for five adult *T. pecari* (USNM), collected by the Smithsonian Venezuelan Project from the states of Apure and Bolívar, and two adult *T. tajacu* (CONN), from Sgto. Rodriguez, Depto. Nueva Asunción, Paraguay, respectively: Length of head + body, 1049.6 and 841; length of tail, 38.2 and 55.0; length of hind foot including hoof, 220 (N = 1) and 188; height of ear from notch, 82.0 and 92.0. One of the foregoing *T. pecari* weighed 26.9 kg. The greater size and weight of *C. wagneri* are obvious except for length of head + body. The overlap of this measurement with that of *T. pecari* reflects the relatively short postcranial dimensions of *C. wagneri*. The greater size of the Taguá's head is responsible for the saying among hunters in the Chaco that when the head is cut off, one is left with only half the animal. Larger cranial size in the Taguá is illustrated by comparing the greatest length of skulls of adult *C. wagneri* with those of *T. pecari*, all CONN specimens from Paraguay: 309.9 (O.R., 298-324; N = 29) and 271.7 (254-282; N = 20).

The ratio of distal to proximal elements of the limbs of *C. wagneri* is comparable to *Platygonus compressus* and *Mylohyus nasutus*, rather than to *Tayassu* (see Table 4). This type of comparison, made by Guilday et al. (1971:291), assumes that the ratio of length of scapula to humerus or the ratios of lengths

of the more distal limb elements to the humerus or femur are all greater in more cursorial mammals. Although limb bones in *C. wagneri* are shorter than in *C. compressus*, their measurements are generally nearer those of the latter species than of either *Tayassu*. Comparative mean lengths of metapodials of *C. wagneri* (Table 1) and *C. compressus* (Welsh Cave, Kentucky), respectively, follow: Metacarpal III, 67.4 and 85.5; metacarpal IV, 69.8 and 86.3; metatarsal, 82.4 (IV) and 91.1. In *C. wagneri*, metatarsals II and V are vestigial; phalanges and hooves for these digits are lacking. In *Platygonus*, metatarsal II is vestigial and V is lacking; in *Tayassu*, II is complete and V is vestigial (Guilday et al., 1971:291). As in *Tayassu*, digits II and V of the forefoot of *C. wagneri* are complete with hooves, phalanges, and articular surfaces on the distal ends of metacarpals. In addition to the evidence of limb proportions, the digits of *C. wagneri* suggest a species that is more cursorial than *Tayassu* but less cursorial than *Platygonus*.

HAIR: The dorsal hairs or bristles, reaching 220 mm, are longer than in other peccaries (Fig. 5). The basal third to half (65-100 mm) of the shaft, strikingly paler than the terminal portion, is indistinctly banded by alternate shades of grayish-tan and off-white. This pale portion gradually merges into a band of dark brown (15-20 mm), followed by a narrower band of white (8-13 mm), and then by a long (65-80 mm) apex of dark brown to black. The shorter, less numerous hairs range from entirely dark brown or black for the shortest (approximately 40 mm) hairs to those with a beginning of a banded pattern. Pronounced apical fraying results in a plumose termination in all but the shortest hairs. In *T. pecari*, hair has a much

Table 4. Relative scapula and limb proportions of selected Tayassuidae; measurements in parentheses. Data for *C. wagneri* (Y CONN 17803 and 18006) are from this study and for all other species, from Guilday, Hamilton, and McCrady, 1971:291.

Skeletal element	<i>Tayassu tajacu</i>	<i>Tayassu pecari</i>	<i>Platygonus compressus</i>	<i>Mylohyus nasutus</i>	<i>Catagonus wagneri</i>
scapula	95%	90%	99%	—	99%
humerus					(171.6/173.9)
radius	69%	72%	78%	84%	81%
humerus	(95.6/138)	(119/166)	(160/206)	(182/217)	(140.6/173.9)
metacarpal IV	36%	38%	45%	47%	40%
humerus	(49/138)	(63.3/166)	(92.1/206)	(103/217)	(70.2/173.9)
tibia	94%	94%	99%	105%	101%
femur	(135/144)	(161/172)	(198/201)	(230/216)	(177.0/175.0)
metatarsal IV	41%	—	46%	53%	47%
femur	(59/144)	—	(92.4/201)	(115/216)	(82.6/175.0)



Fig. 5. Dorsal hair of peccaries; left, *C. wagneri*; middle, *T. tajacu*; right, *T. pecari*.

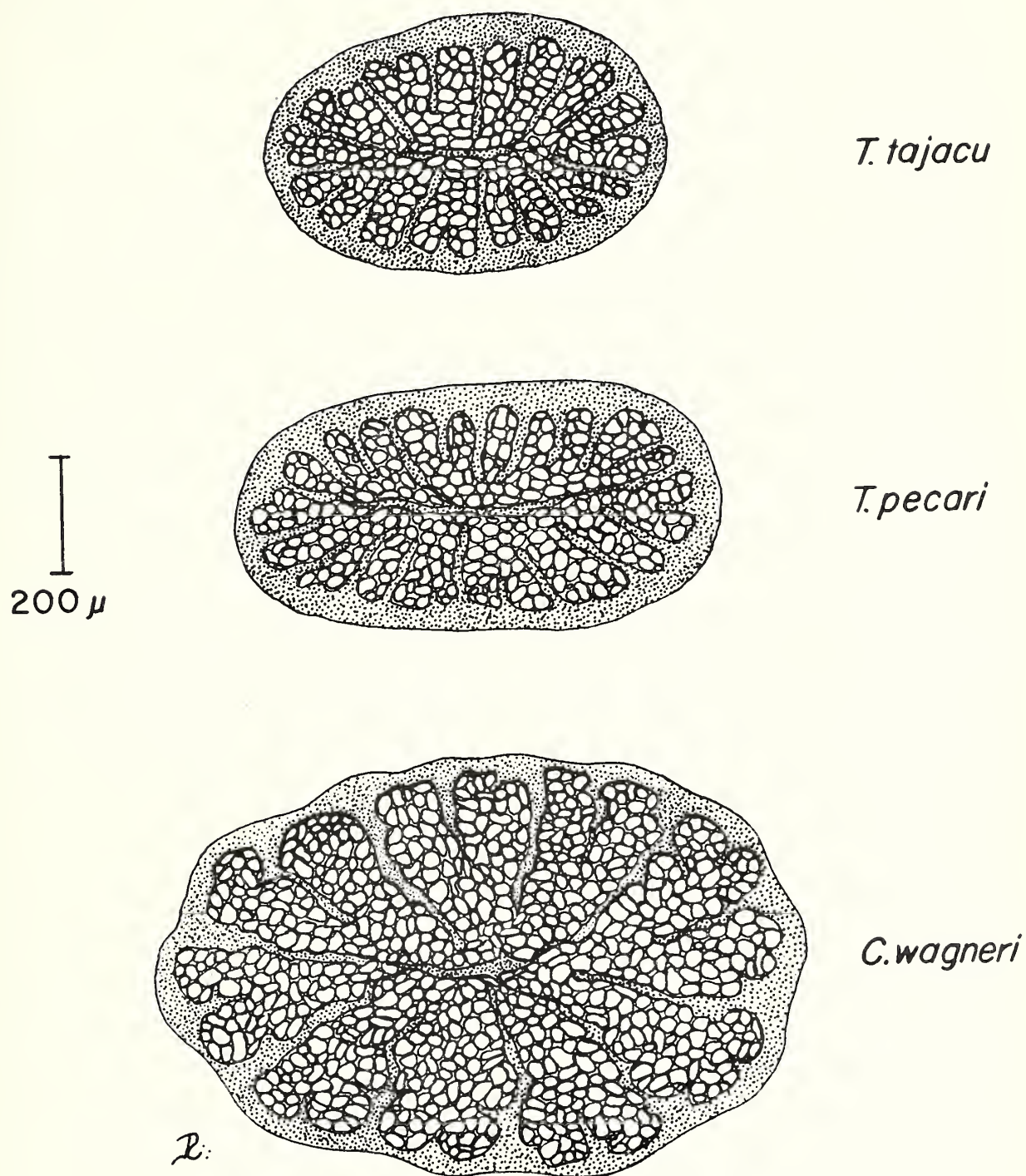


Fig. 6. Hair of the peccaries; cross sections of dorsal hair at middle of shaft. Note the undulating surface and thinner cortical layer for *C. wagneri* as compared with the smaller diameter, smooth surface and thicker cortical layer for *T. tajacu* and *T. pecari*.

shorter pale basal area, followed by dark brown to black on the remaining three-quarters of the shaft. In *T. tajacu*, hair lacks the pale basal portion entirely, having instead, a series of distinct contrasting bands of alternating light and dark along the shaft before the terminal dark tip. Hair is also much shorter than that of *C. wagneri*, not exceeding 150 μ m in all specimens examined from Paraguay. The shortest hairs of *T. tajacu* are white rather than black, as in *C. wagneri*.

Scanning electron micrographs indicate that in *C. wagneri* the hair surface has undulations or shallow grooves that are absent in both *Tayassu*. This feature can be seen better in cross sections prepared for light microscopes. Figure 6 illustrates these undulations, the larger diameter, and thinner cortical layer of *C. wagneri*. I measured diameter and minimal depth of the cortical layer, between the internal radial ribs, at the base, middle, and tip of hairs of the three peccaries. The thinness of the cortical layer in *C. wagneri* is illustrated by the means (in microns) and the ratio of minimal depth of the cortical layer to greatest diameter of the section as follows: *C. wagneri*, 17 (O.R., 15-20; N = 14) and .02 (.02-.03; N = 12); *T. pecari*, 37 (30-50; N = 20) and .06 (.05-.12; N = 10); *T. tajacu*, 28 (20-35; N = 11) and .06 (.05-.06; N = 9).

SEXUAL DIMORPHISM: Since most specimens of the Chacoan peccary are skulls from hunters' kills, sexes are chiefly unknown, but it is obvious that the variation of the canines and surrounding bone is not as extreme as in *P. compressus*. Coefficients of variation for *C. wagneri* and for *P. compressus* (Guilday et al., 1971: 293) are respectively: Width across upper canines, 2.86 and 10.65; width across canine buttresses, 3.03 and 12.26. When the sample of adult *C. wagneri* is divided by a combination of size of canines and width across canines, the group with the larger canines has a wider skull and somewhat shorter postcanine diastema and condylobasal length. The magnitude of variation is reduced by this segregation, a major reduction occurring in the zygomatic breadth from $s = 10.8$ for the unstratified group to $s = 4.4$ for the large-canine group, and 2.1 for the small-canine group. I am reluctant to associate size of canines with sexual dimorphism in *C. wagneri* because of the lack of clear-cut separation of "males" and "females." Since the more gracile skull of *C. wagneri* lacks the extreme development of canine buttresses and has less variation in canines, the possible effects of both age and any sexual differences are less accentuated than in *P. compressus*.

EXTERNAL NARES: Height of the nasal opening is greater in *Catagonus* than in *Tayassu*, as follows, with the mean, if given, followed by s : *Catagonus metropolitanus* 38; *C. carlesi* 28; *C. wagneri* 31.2, 1.2 (O.R. = 29.0-33.3; N = 23); *Tayassu pecari* 24.8, .80 (23.3-26.6; N = 18); *T. tajacu* 20.7, .71 (19.7-22.5; N = 18). In *Catagonus wagneri*, *C. carlesi*, *Platygonus compressus*, *P. cumberlandensis*, and *Tayassu pecari*, the most posterior lateral margin of the nares (= narial notch) is well posterior to I^2 . In *T. tajacu* the narial notch is broader, not so deep, and falls above the posterior part of I^2 . In *T. pecari* the narial notch differs from both *T. tajacu* and *C. wagneri* in being acuminate. *C. wagneri* differs from both *T. pecari* and *T. tajacu* in having a broadly curved midlateral projection, a process of the premaxilla, which divides the narial notch into subequal dorsal and ventral arcs. Where a slight projection occurs in the narial notch of *T. pecari* and *T. tajacu* from Paraguay, the projection is formed by the nasal bone rather than the premaxilla.

ROSTRUM: The much greater size of the rostrum, in both actual measurement and in proportion to the postrostral length of skull, separates *Catagonus* and *Platygonus* from the shorter-nosed members of *Tayassu*. Note in Table 5, however, that the postrostral to rostral ratios of *Platygonus* from the Lower Pleistocene of Argentina are approximately midway between *Tayassu* on one hand and *Platygonus* of North America and *Catagonus* on the other. The ratio of *Platygonus* sp. (MHN 305) is nearest to ratios of *Tayassu*.

The lateral profile of the rostrum in *Catagonus*, *Platygonus compressus*, and *P. cumberlandensis* is distinctly convex. The rostrum in *Tayassu pecari* is slightly concave in profile; in *T. tajacu*, *Platygonus scagliai*, *P. chapadmalensis* (MMCN 246), and *Platygonus* spp. (MHN 305, MMCN 1212), slightly convex or straight. In transverse section, the dorsum of the rostrum is broadly rounded in *Catagonus* and *Platygonus*, more sharply rounded in *T. tajacu*, and flat in *T. pecari*.

Woodburne (1968:28) used the well-defined anterior portion of the supraorbital canals in *T. tajacu* as a distinction between that species and *T. pecari*. In Paraguayan specimens of *C. wagneri* and *T. pecari*, the anterior portion of the canals varies from indistinct to, in the older specimens, as deep and well defined as the canals in *T. tajacu*. The anterior portions of the canals are also well defined in *Platygonus scagliai*, *P. chapadmalensis* (MMCN 246), *Platygonus*

Table 5. Comparison of ratios* of postrostral to rostral length and of position of infraorbital foramen to rostral length for *Catagonus*, *Platygonus*, and *Tayassu*. See text for explanation of abbreviations.

	PRL / RL adj.	Orbit to infraorbital foramen / RL
<i>Catagonus wagneri</i> , Recent	.37, s .02, N 15	.47, s .02, N 14
<i>Catagonus</i> sp., MMCN 41, Mid-Pleist., Argentina	.36
<i>Platygonus compressus</i> , CM 12885, 12886, 20114, U-Pleist., N. Am.	.37 (. . . , .37, .38)	.44 (.46, .43, .44)
<i>P. cumberlandensis</i> , USNM 8000, 8146, 8147, Mid-Pleist., N. Am.	.36 (.38, . . . , .33)	.42 (.40, .43, . . .)
<i>Platygonus</i> sp., MMCN 1212, L-Pleist., Argentina	.48	.41
<i>P. scagliae</i> , MMCN 156, L-Pleist., Argentina	.48	.41
<i>P. chapadmalensis</i> , MMCN 246, L-Pleist., Argentina	.48	.31
<i>Platygonus</i> sp., MHN 305, Pleist., Brazil	.51	.30
<i>Tayassu tajacu</i> , Recent	.59, s .02, N 17	.30, s .02, N 19
<i>T. pecari</i> , Recent	.60, s .03, N 13	.23, s .01, N 17

*Measurements for *C. wagneri* are from Table 1. Pertinent measurements for other specimens follow. Measurements in parentheses are for individual specimens; \bar{Y} , s, and N are given for *T. tajacu* and *T. pecari*.

	PRL	RL adj.	Orbit to infra- orbital foramen	RL
<i>Catagonus</i> sp.	71	195	...	200
<i>P. compressus</i>	76 (. . . , 74, 77)	202 (. . . , 202, 202)	90.5 (93, 88, 90)	205.8 (203, 207, 207)
<i>P. cumberlandensis</i>	90 (97, . . . , 82)	251 (255, . . . , 246)	111 (103, 119, . . .)	261 (260, 275, 250)
<i>Platygonus</i> sp.	112	232	97	237
<i>P. scagliae</i>	92	178	72	184
<i>P. chapadmalensis</i>	91	190	61	194
<i>Platygonus</i> sp.	97	190	58	194
<i>Tayassu tajacu</i>	73.7, 4.7 N=17	124.8, 6.1 21	35.1, 2.9 19	127.5, 6.1 22
<i>T. pecari</i>	88.8, 3.7 N=13	150.2, 6.4 18	38.5, 3.5 19	153.0, 5.1 19

sp. (MMCN 1212), and in the lateral views of *P. stenocephalus* (Winge, 1906: Plate 6), and *Catagonus carlesi* (Rusconi, 1930: Plate 3). All these specimens from the Pleistocene were adults with evident molar wear. Thus the definite outline or sculpturing of the anterior canals, per se, is not a unique character of *T. tajacu* or *Dicotyles* vs. *Tayassu*, and especially not of older animals. The anterior canals of *T. tajacu*, being located nearer the summit of the dorsal rostral curve, are more evident from dorsal view. The anterior canals of *C. wagneri*, *P. compressus*, and *T. pecari* are located more laterally on the rostrum and are thus more broadly separated than the constricted anterior canals of *T. tajacu*. The anterior canals shown for *C. carlesi* by Rusconi (1930: Plates 3, 4) appear to be within the range of variation of *C. wagneri*, and

should not, in my view, be used as evidence of relationship of *C. carlesi* to *T. tajacu* as Woodburne (1968:32) suggested.

INFRAORBITAL FORAMEN (Table 5): In *C. wagneri* and *C. carlesi*, the anterior opening of this foramen is almost halfway between the orbit and the tip of the premaxilla, lying above P¹. This position is approximated in *Platygonus* from North America and in some of the specimens from South America, such as *P. scagliae* and *Platygonus* sp. (MMCN 1212). The remaining specimens from South America, *P. chapadmalensis* (MMCN 246) and *Platygonus* sp. (MHN 305), are similar in this respect to *T. tajacu*. In both species of *Tayassu* the opening is in the posterior third of the rostrum, above P¹ or M¹. In *T. tajacu* it lies under the anterior part of the zygomatic arch, and in

Table 6. Comparison of suborbital zygomatic depth in Recent peccaries from Paraguay, and specimens from the Pleistocene of Argentina, Brazil, and North America. See text for explanation of abbreviations.

	Suborbital zygomatic depth	Ratio of suborbital zygomatic depth / PRL
<i>Platygonus cumberlandensis</i> , USNM 8000, Mid-Pleistocene, North America	79.6	.82
<i>Platygonus chapadmalensis</i> , MMCN 246, Lower Pleistocene, Argentina	42.8	.47
<i>Platygonus</i> sp., MMCN 1212, Lower Pleistocene, Argentina	49.6	.44
<i>Platygonus scagliae</i> , MMCN 156, Lower Pleistocene, Argentina	39.1	.42
<i>Platygonus</i> sp., MHN 305, Pleistocene, Brazil	39.0	.40
<i>Platygonus compressus</i> , AMNH 42781 & TUC 5-1277, Upper Pleistocene, North America	35.0 (35.0, 35.0)	.44 (.44, .45)
<i>Catagonus wagneri</i> , Recent, Paraguay	30.3, s 2.3, N 30	.43, s .04, N 15
<i>Catagonus</i> sp., MMCN 41, Mid-Pleistocene, Argentina	25.7	.36
<i>Tayassu pecari</i> , Recent, Paraguay	22.8, s 1.6, N 21	.26, s .02, N 13
<i>Tayassu tajacu</i> , Recent, Paraguay	17.5, s 3.9, N 22	.24, s .05, N 17

T. pecari, even more posteriorly, well under the zygomatic shelf. The transverse shape of the opening differs in all three Recent species. In *C. wagneri* the opening is ovoid and oriented vertically along its longest axis; in *T. tajacu*, the longest axis of the oval is directed dorsolaterally; in *T. pecari* the opening is narrow and slit-like.

ZYGOMA: In both *Tayassu pecari* and *T. tajacu*, the ventrolateral face of the maxillary zygomatic process is deeply excavated as the fossa for the *dilator naris lateralis* muscle (as described for *T. tajacu* by Woodburne, 1968) and the fossa extends anteriorly above the opening of the infraorbital foramen. *Catagonus wagneri*, *C. carlesi*, and *Platygonus compressus* differ markedly from *Tayassu* in having only a shallow, short fossa not extending anteriorly beyond the infraorbital foramen.

Vertical depth of the suborbital zygoma is much greater in *Catagonus* and *Platygonus* than in *Tayassu*. This is shown, both as ratios and as measurements, in Table 6. Depth of the suborbital zygoma is, however, less in the more gracile skull of *Catagonus* than in *Platygonus*. In *C. wagneri* and *Catagonus* sp. (MMCN 41), the suborbital zygoma lacks the distinct concavity on the lateral face found in *Platygonus*.

ORBITS: In *Catagonus* and *Platygonus*, the orbits lie posteriorly in the skull; the anterior margin of the

orbit is distinctly posterior to the last molar; and the postorbital process of the zygomatic is dorsal to the glenoid fossa. In both *Tayassu*, the anterior margin of the orbit lies above either the M² or M³ and the postorbital process of the zygomatic is well anterior to the preglenoid process. In *Catagonus* and *Platygonus* the eyes are thus set posteriorly behind a much longer rostrum, while in both *Tayassu*, eyes are more anteriorly positioned behind a shorter rostrum. A mid-horizontal line through the orbits of either *Tayassu* is dorsal to the anterodorsal tip of the rostrum.

In the genera *Catagonus* and *Platygonus*, compensatory shift in the orbital position took several evolutionary pathways that probably reduced interference of the longer rostrum with vision: (1) The entire frontal region, including the orbits, shifted dorsally well above the dorsal margin of the rostrum, as in *Platygonus scagliae*, *P. chapadmalensis* (MMCN 246), and *Platygonus* sp. (MMCN 1212). (2) Only the orbits became positioned more dorsally, nearer the upper margin of the skull, as in *Platygonus cumberlandensis* and *P. compressus*, as pointed out by Guilday et al. (1971:298). (3) The long axis of the orbits came to lie at a more oblique angle to the long axis of the skull, as in *Catagonus* and *Platygonus* except for *P. scagliae* and relatives, above. This position of the eyes, along with the basicranial flexure of the

Table 7. Comparison of cranial capacities of Recent peccaries, *Catagonus wagneri*, *Tayassu pecari*, and *T. tajacu*. All specimens are adults from Paraguay. See text for definitions of abbreviations.

Species	\bar{Y}	s	C	O.R.	N
Cranial capacity, ml.					
<i>C. wagneri</i>	114.1	7.9	6.9	102-130	22
<i>T. pecari</i>	158.9	5.1	3.2	150-167	9
<i>T. tajacu</i>	95.9	6.2	6.5	84-105	10
Cranial capacity / Condylbasal length					
<i>C. wagneri</i>	.42	.03	6.6	.37-.51	21
<i>T. pecari</i>	.67	.03	3.8	.62-.70	9
<i>T. tajacu</i>	.50	.04	7.5	.43-.53	8

skull discussed next, would permit forward vision when the head flexed in a feeding position, permitting less interference by the rostrum (see Guilday et al., 1971:304). (4) The eyes shifted to a more lateral position, e.g., as Guilday et al. (ibid:298) found for *Platygonus*.

SIZE OF BRAIN CASE: Measurements of cranial capacity (Table 7) indicate a proportionally much smaller brain than in *Tayassu*. The smaller skull of *T. pecari* has a greater cranial capacity than *C. wagneri*, while the O.R. of the cranial capacity of the smallest species, *T. tajacu*, overlaps with that of the large *C. wagneri*. The markedly lower ratio of cranial capacity to condylbasal length in *C. wagneri* is similar to its low ratio of postrostral length to rostral length, adjusted (Table 5). Both ratios are expressions of the long rostrum and short postrostral dimension in *C. wagneri*. It will be noted in Tables 1 and 5 that the postrostral lengths of the crania of *Catagonus* and *P. compressus* are much shorter than that measurement in *T. pecari*, and that the ratios of PRL/RL adj. in *Catagonus* and *Platygonus* are significantly lower than those in *Tayassu*. It is therefore to be expected that when the cranial capacities are estimated for fossil *Platygonus* and *Catagonus*, they will prove to have had proportionally smaller brains than *Tayassu*. This would have conferred a distinct advantage upon *Tayassu*, although Guilday et al. (1971:309, 311) doubt that *Tayassu* and *Platygonus* could have been competitors in North America. It is difficult to imagine, however, that *Catagonus* and *Tayassu* were not competitors in the shifting ecotone between forest and forest-edge habitats in South America. In all but dusty, open habitats, the greater success of *Tayassu* must have been assured.

BASICRANIAL FLEXURE: Distinct basicranial flexure, absent in *T. pecari* and *T. tajacu*, is remarkable in *Catagonus wagneri*, *Catagonus* sp. (MMCN 41), *Platygonus scagliae*, *Platygonus* sp. (MMCN 1212), *P. cumberlandensis*, and *P. compressus*. In these species the basioccipital region is directed more anterodorsally, and the basisphenoid, with an even more dorsal tilt, approaches the vertical. In Recent *C. wagneri*, the ventral surface of the basisphenoid is 65°-75° from horizontal as defined by the premolar-molar tooththrow, compared to approximately 20° in *Tayassu*. Guilday et al. (1971:304) associated this flexure and the oblique long axis of the orbits in *P. compressus* with evolutionary adaptation for life in more open habitats. Such modifications would permit a horizontal direction of the main axis of sight even when the head was flexed in a grazing attitude. This is a reasonable suggestion, especially when correlated with the extreme rostral development in *Platygonus* and *Catagonus*, which would require cranial flexure for reduced impairment of vision in both grazing and nongrazing attitudes.

SINUSES: Extreme development of the sinuses, a distinctive feature of the skull of *Platygonus* (see Guilday et al., 1971), occurs also in *C. wagneri*. A pair of prominent suborbital sinuses project dorso-laterally to the pterygoid processes and posteriorly to the level of the tympanic bullae. Air passages connect the dorsal side of these sinuses with a posterior extension of the nasal chamber. The extreme posterior margin of the nasal chamber reaches the level, lateral to the midventral line, of the anterior part of the basisphenoid. The well-developed maxillary sinuses, the posterior extension of the frontal sinuses into the dorsal part of the parietal bones, the suborbital sinuses,

Table 8. Comparison of mandibles, *Catagonus*, *Platygonus*, and *Tayassu*. Where available, \bar{Y} , s, and N, or \bar{Y} and N are given. Mandibular length is from condyle to anterior tip. Measurements of *P. compressus* are from Guilday et al. (1971:293).

Species	Length, mandible	Maximal height ramus	Depth at postcanine diastema	Depth at ant. margin M ₁	Height, ramus L., mandible
<i>C. wagneri</i> , Recent, Paraguay	209.8, 5.7 N = 20	93.0, 3.5 20	23.4, 1.4 23	31.2, 1.8 23	.44, .02 19
<i>Catagonus</i> sp., MMCN 41, Mid-Pleist., Argentina	202	...	30.6	35.8	...
<i>P. compressus</i> , Welsh Cave, U-Pleist., Kentucky	218.1, 6.0 N = 12	94.6, 5.0 10	31.2, 1.5 18	39.0, 2.7 18	.43*
<i>P. cumberlandensis</i> , USNM 8147, 8921-3, Mid-Pleist., Maryland	278.3 N = 4	113 1	36.7 3	48.2 3	.41 1
<i>Platygonus</i> sp., MMCN 1212, L-Pleist., Argentina	270	...	40.9	50.1	...
<i>P. chapadmalensis</i> , MMCN 246, L-Pleist., Argentina	243	...	40.5	49.8	...
<i>P. scagliae</i> , MMCN 156, L-Pleist., Argentina	211	...	31.4	41.7	...
<i>Tayassu pecari</i> , Recent, Paraguay and northern Argentina	189.0, 4.3 N = 14	88.4, 3.3 14	29.2, 2.1 15	38.4, 2.9 15	.47, .02 13
<i>T. tajacu</i> , Recent, Paraguay and northern Argentina	152.4, 8.8 N = 19	72.6, 4.0 16	26.6, 1.4 18	32.2, 1.4 18	.47, .02 16

*ratio of \bar{Y} 's.

and the posterior extension of the nasal chamber result in the brain case of *C. wagneri* being nearly surrounded by air chambers. Finch, Whitmore, and Sims (1972:18) commented on the cul-de-sacs associated with the extreme development of sinuses in *Platygonus compressus*: "The passage of air through the nasal passage was thus very tortuous, which may have been an advantage in a dust-laden atmosphere." It should be added that such extreme development of the sinus-nasal system in *Catagonus* and *Platygonus* could serve as both a dust trap and a well-developed olfactory system, with the latter requiring the former in a dusty atmosphere. *Tayassu pecari* and *T. tajacu*, although sharing the familial development of sinuses about the dorsal and anteroventral part of the brain case, lack this extreme development of sinuses. The size of the cribiform plates, much smaller in *Tayassu*, also suggests a lesser dependence upon olfaction than in *Platygonus* and *Catagonus*.

MANDIBLE: As with the cranium, the mandible of *C. wagneri* is somewhat shorter than it is in the smallest *Platygonus*, and much longer than in the largest *Tayassu* (see Table 8). The body of the mandible is so slender that the depth is actually less than in the smallest peccary, *T. tajacu*. In both *Tayassu*, the

mandible is proportionally deeper and has a higher ratio of height of ramus to total length than in *Catagonus*, *P. compressus*, and *P. cumberlandensis*.

In *Tayassu*, the posterior margin of the mandible bulges distinctly beyond the condyles, but in *Catagonus* and *Platygonus*, it projects only slightly if at all. In the more massive skull of *Platygonus*, the angular process of the mandible flares laterally, in contrast to *Catagonus* and *Tayassu*, where the angular portion is deflected medially in a gentle curve, or is vertical. Like *Tayassu*, *C. wagneri* lacks the distinctive keel on the mandibular symphysis found in *P. cumberlandensis* and *P. compressus*. A slight keel is observable on the holotype of *P. scagliae* and on *P. chapadmalensis* (MCN 246). Of the specimens of North American *Platygonus* examined, only those from the Upper Pliocene (Hemphillian) lacked a keel: Edson Quarry, Kansas (AMNH), Snake Creek Formation, Nebraska (AMNH), and Hagerman Formation, Idaho (USNM 13798). This keel and the lateral flare of the angular processes seem to be specialized features of the Middle to Upper Pleistocene radiation of *Platygonus* in North America, not occurring in the more gracile skulls of earlier *Platygonus* or the more conservative *Catagonus*.

SIZE OF TEETH AND DIASTEMAS: Despite the smaller

skull of *C. wagneri*, the teeth are larger than in many species of *Platygonus* and are proportionally larger than in any member of that genus. The maxillary tooththrows of *C. wagneri* and *P. compressus* are compared in Figure 3. This longer tooththrow is accommodated in the shorter jaw of *C. wagneri* through a reduction in length of diastemas. This is illustrated in Figure 7, where the maxillary postcanine diastema is plotted against the length of M^{1-3} . The premolars of *C. wagneri* are frequently at oblique angles to the main axis of the tooththrow. I presume this is an effect of crowding caused by phylogenetic reduction of length of jaw not entirely compensated by reduction in diastemal space.

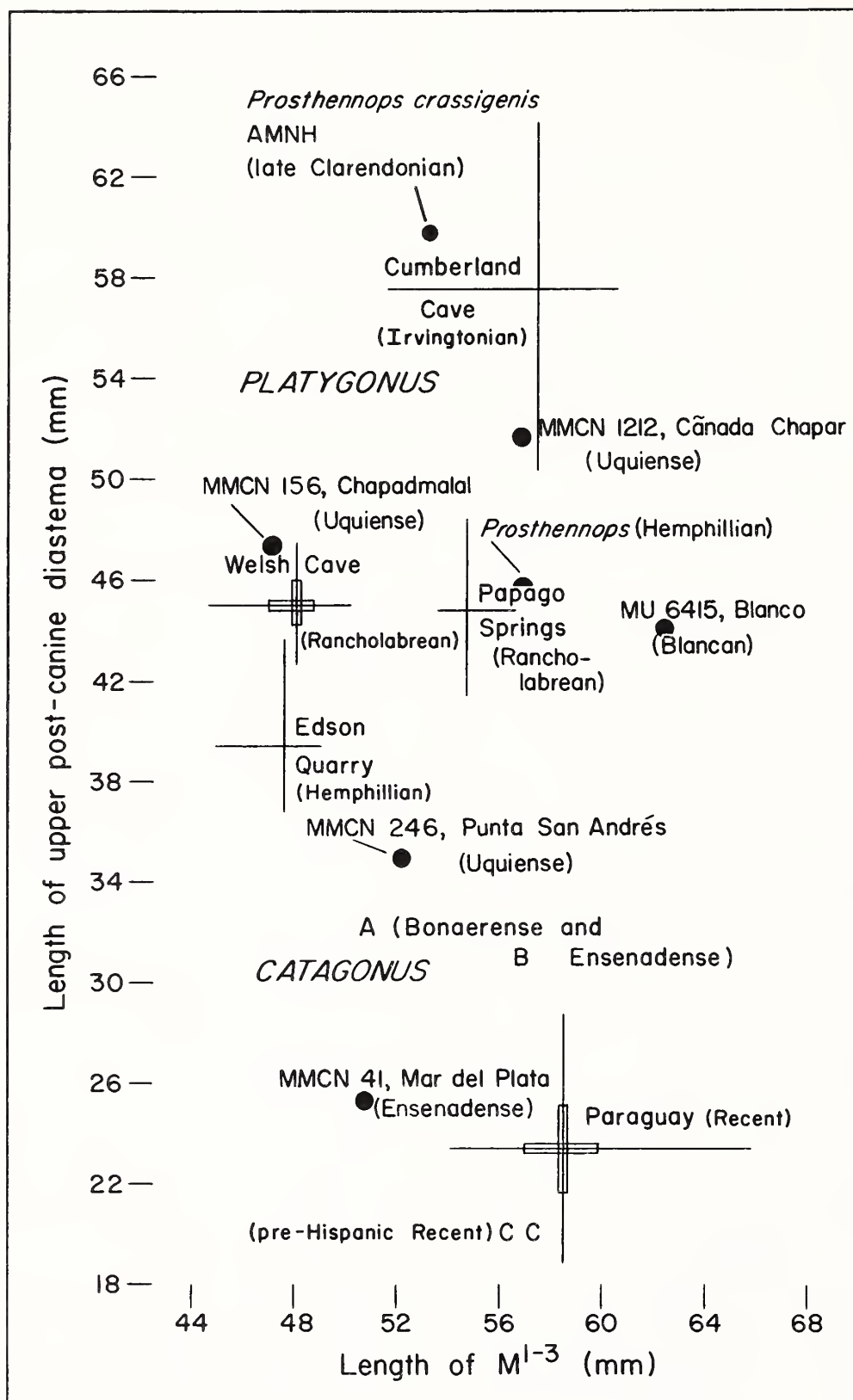
CUSPS AND CINGULA: The teeth of *Catagonus* are similar to *Platygonus* in being functionally lophodont and more hypsodont than in *Tayassu*. As shown in Figures 3 and 4, the premolars and molars of *C. wagneri* have numerous small cusps in addition to the major cusps that are characteristic of *Platygonus*. The cingula are well developed and surround the anterior, buccal, and posterior margins of P^2 - M^3 . Similar cuspsules and well developed cingula occur in the holotype of *C. wagneri* (Rusconi, 1930: Plate 16) and on P^2 - M^1 of *C. metropolitanus* (ibid.: Plates 8 and 9). Wear on the teeth of *C. carlesi* (ibid.: Plate 5) prevents inspection for cingula and cuspsules. Although teeth of the holotype of *C. bonaerensis* are also worn, I was able to see pronounced cingula on the anterior faces of $M^{2,3}$ and $M_{2,3}$ and cuspsules at the boundaries between the anterior and posterior moieties of P_4 and M_2 . In North American *Platygonus*, cingula on the buccal side of the molars are less well developed than in *Catagonus*. It should be noted, however, that in the temporal sequence of *Platygonus* examined, the buccal cingula of molars were more evident in the Blancan and Irvingtonian specimens than in the later Rancholabrean. Buccal cingula of the molars occur in the holotypes of *Platygonus marplatensis* and *P. scagliae*, in *P. chapadmalensis* (MMCN 246), and the large *Platygonus* sp. (MMCN 1212). These specimens from the Upper Pliocene to Lower Pleistocene of Argentina, therefore, are intermediate in this character between *Catagonus* and North American *Platygonus*. In both *Catagonus* and *Platygonus*, cingula of the P^{2-4} are well developed on the anterior and posterior faces and, for *Catagonus*, the buccal face and for *Platygonus*, the lingual face. In the mandible, no pronounced cingula occur on P_{2-4} of *Catagonus* or *P. compressus*, but are well developed on the anterior, posterior, and buccal surfaces of $P_{3,4}$ of *P. cumber-*

landensis. *Tayassu* differs markedly from both *Catagonus* and *Platygonus* in lacking such well-developed cingula on premolars and molars. Where cingula do occur, they are restricted to portions of the anterior and posterior faces.

INCISORS: The incisors of *C. wagneri* are longer and the maxillary incisors more procumbent than are those of the other living peccaries. Across the posterior base of each incisor is a cingulum, absent in *T. pecari* and present on only the upper incisors of *T. tajacu*. A minute median cuspsule, rather than a cingulum, is present on the unworn posterior face of the lower incisors of Paraguayan *Tayassu*. The unworn I^2 of *C. wagneri* differs from that of *Tayassu* in having a rounded tip, crenulated on its posterior margin, and a cavity in the occlusal (posterior) surface. A slight ridge partially divides the cavity into medial and lateral halves. The I^2 of *Tayassu* has a pointed tip without crenulations and without the cavity or median ridge on the posterior surface.

The size of the I^2 , as measured transversely at the alveolus to avoid the effects of wear, does not differ greatly among *Catagonus*, *Tayassu*, and *Platygonus* from the Lower to Mid-Pleistocene of South America. However, I^2 's in North American *Platygonus* from the Middle to Upper Pleistocene are smaller. The latter teeth are compared with *Catagonus*, with \bar{Y} and s given where available: *C. wagneri*, 6.1 and .37 (O.R., 5.5-8.6; $N = 15$); *Catagonus* sp. (MMCN 41), 6.8; *P. cumberlandensis*, 5.2 (4.9, 5.5; $N = 2$); *P. alemanii*, Papago Springs, 5.5 (5.2-5.9; $N = 4$); *P. compressus*, Welsh Cave, 4.6 (3.3-5.6; $N = 5$). The statement of Guilday et al. (1971:305) that the I^2 of *Platygonus* is "... reduced to a small peg ..." reflects the small size of this tooth in some of the specimens from Welsh Cave.

As in *Tayassu*, all specimens of *C. wagneri* from Paraguay have three pairs of lower incisors, whereas I_3 is rarely present in North American Pleistocene *Platygonus*. One (CM 2634) of 15 undamaged mandibles of *P. compressus* from Welsh Cave has alveoli for I_3 . One (AMNH 45719) of seven undamaged mandibles of the same species from Cherokee Cave, Missouri, has an alveolus for the left I_3 . Of four complete mandibles of *P. cumberlandensis*, one (USNM 8147) has vestigial alveoli for I_3 . The following intact mandibles of *Platygonus* from the North American Upper Pliocene have alveoli for I_3 : One (USNM 13798) from the Hagerman Formation and six of seven specimens (AMNH) from Edson Quarry, Kansas. The small sample from the Pleistocene of Argen-



tina suggests a more conservative character: *Catagonus* sp. (MMCN 41) and *Platygonus* sp. (MMCN 1212) have I_3 on both right and left; *Catagonus* sp. (MMCN 707) and *P. scagliae* have I_3 or an alveolus present on only the right side; *P. chapadmalensis* (MMCN 246) has no alveolus for the right I_3 and probably none for the left.

CANINES: The canines of *Catagonus* and *Platygonus* are similar in being longer from alveolus to tip, and, in proportion to that length, more slender than the shorter, broader canines of *Tayassu*. The base of the canine in *C. wagneri* and *P. compressus* is smaller than in *T. pecari* and, as would be expected, in those peccaries with larger skulls such as *P. cumberlandensis* and *C. metropolitanus*. Anteroposterior and transverse diameters of the upper canine at its alveolus follow: *Platygonus alemanii*, Papago Springs, 14.2 and 10.4 ($N = 4$); *Catagonus wagneri*, Paraguay, 15.1 and 10.4 ($N = 24$ and 23); *C. wagneri*, holotype, 15.5 and 10; *C. carlesi*, holotype, 15.5 and 11; *C. metropolitanus*, 21 and 14; *P. cumberlandensis*, 20.0 and 14.3 ($N = 3$); *Tayassu pecari*, 16.3 and 11.0 ($N = 9$ and 10); and *T. tajacu*, 14.0 and 9.7 ($N = 17$).

P^2 : The first upper premolar of *C. wagneri* is multicusped and ovoid, with the anteroposterior diameter greater than the transverse. In *Platygonus*, the P^2 is bicusped and has equal diameters; in *Tayassu*, the P^2 is roughly triangular in shape, its apex being an anterior lobe formed by the single large cusp. The anteroposterior diameter of *Catagonus*' P^2 , although larger in proportion to its transverse diameter than in *Platygonus*, is approximately the same as in those *Platygonus* with large crania: *C. wagneri*, Paraguay, 11.4 (O.R., 10.1-12.8; $N = 29$); *Platygonus* sp. (MMCN 1212), 11.3; *P. cumberlandensis*, holotype and paratypes, 11.4 ($N = 5$); *P. texanus* (MU 6415), 10.9; *P. bicalcaratus* (TMM 31175-12), 11.3.

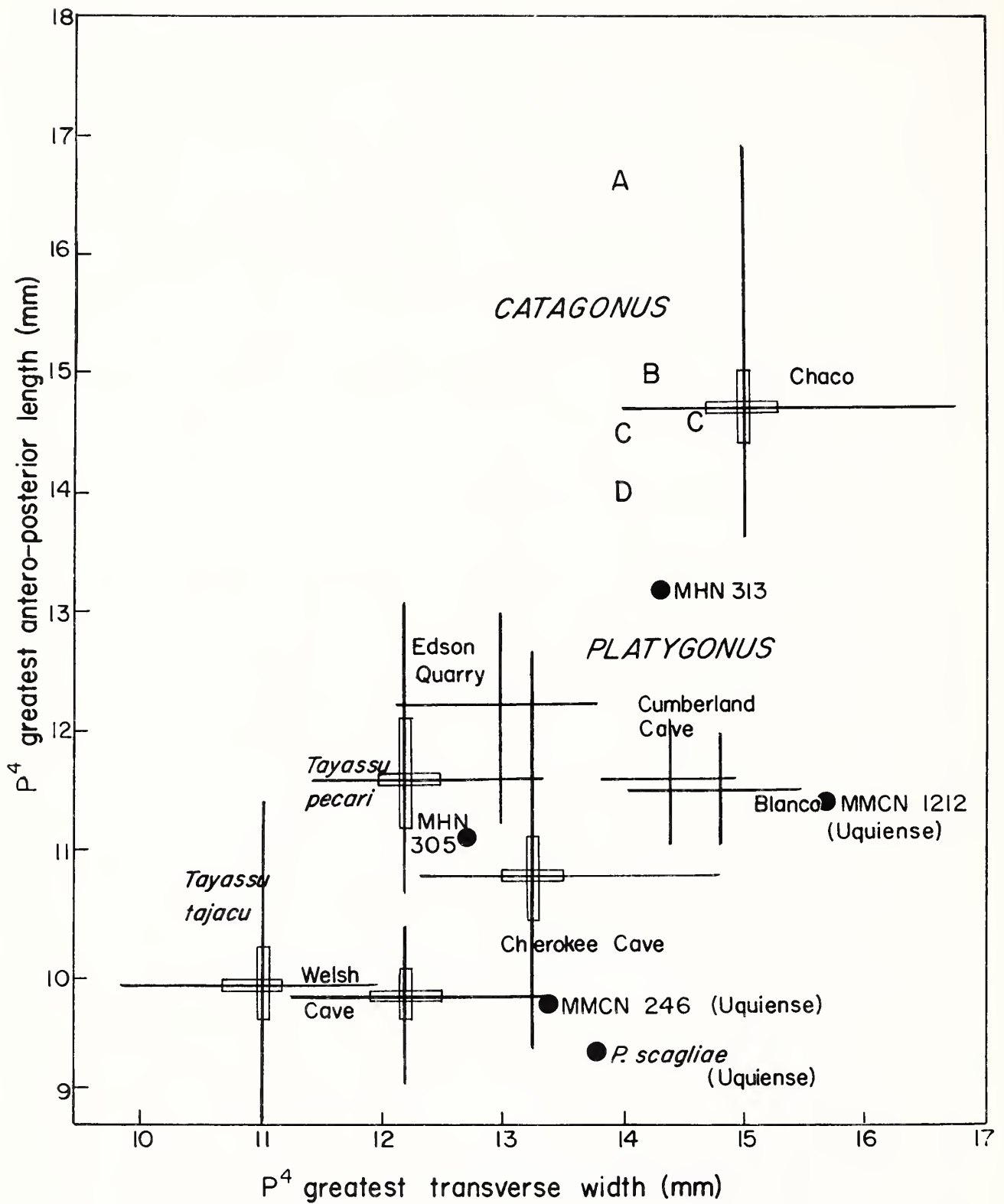
P_2 : The first lower permanent premolar of *Catagonus* is proportionally narrow and has a single tall major cusp preceded by a low cuspsule and followed by poste-

rior cuspsules (Fig. 4). As in *Tayassu*, the P_2 lacks the laterally paired major cusps of *Platygonus*, but such cusps are present in the deciduous P_2 of *C. wagneri*.

P^3 : The second upper premolar of *C. wagneri* has three major cusps, a variably larger number of cuspsules, and definite cingula on the anterior, buccal, and posterior margins. It shares the character of three major cusps with *Tayassu*, and differs from *Platygonus* whose P^3 has two major cusps, transversely arranged, and a complete cingulum on the lingual instead of the buccal margin. Although the P^3 of *C. wagneri* is much larger than in *Tayassu*, *Prosthennops*, *Platygonus compressus*, *P. scagliae*, *P. chapadmalensis*, and *Platygonus* sp. of Edson Quarry, the O.R.'s of both diameters overlap with the diameters of *Platygonus* sp. (MMCN 1212), *P. cumberlandensis*, *P. texanus* (MU 6415), and *P. bicalcaratus* (TMM 31175-12). The P^3 of *Prosthennops* differs in being narrower; those of most *Platygonus* are wider than long; and those of *C. wagneri*, approximately equal in both diameters. This range is indicated by the following examples of ratios of transverse to anteroposterior diameter: *Prosthennops edensis*, .94; *Prosthennops* sp., Mixon Bone Beds, .92; *P. crassigenis*, .86 ($N = 2$); *Platygonus* sp. (MMCN 1212), 1.09; *P. chapadmalensis* (MMCN 246), 1.09; *P. compressus*, Welsh Cave, 1.11 (from \bar{Y} 's of Guilday et al., 1971); *P. cumberlandensis*, 1.13 (O.R., 1.09-1.16; $N = 5$); *P. texanus* (MU 6415), 1.13; *Catagonus wagneri*, Paraguay, 1.00 (.88-1.11; $N = 32$).

P_3 : Although similar to P_2 , the second lower premolar of *C. wagneri* differs in being larger and in having the central, major cusp partially separated into lateral subdivisions. This is suggestive of the two transversely oriented cusps of *Platygonus* and *Tayassu*. The P_3 differs, like that of *Tayassu*, in lacking a cingulum, as contrasted with *Platygonus* in which a cingulum is continuous from the anterior and buccal to posterior face. Also like *Tayassu* but differing from *Platygonus*, the main cusp is preceded and followed by smaller cusps. The unworn anterior cusp of *C.*

◀ Fig. 7. Comparison of Recent and fossil *Catagonus* with *Platygonus* and *Prosthennops*. A single line represents the observed range; a bar represents two standard errors of the mean of sample. Measurements are from this study and the literature, as follows: *Catagonus*: A, *C. carlesi*, holotype, Prov. Santiago del Estero (Rusconi 1930); B, composite, M^{1-3} of *C. bonaerensis* and diastema of *C. metropolitanus*, Prov. Buenos Aires (ibid.); C, *C. wagneri*, holotype and paratype, Prov. Santiago del Estero (Rusconi 1948); MMCN 41, *Catagonus* sp., Prov. Buenos Aires; Paraguay, *C. wagneri*, Recent ($N = 27$ X and 31 Y). *Platygonus*, reading from top down: Cumberland Cave, Maryland, *P. cumberlandensis*, holotype and paratypes ($N = 4$); MMCN 1212, *Platygonus* sp., Prov. Buenos Aires; MMCN 156, *P. scagliae*, holotype, Prov. Buenos Aires; Welsh Cave, Kentucky, *P. compressus* (Guilday et al. 1971); Papago Springs, Arizona, *P. alemanii* ($N = 3$); MU 6415, *P. texanus*, Blanco Beds, Texas; Edson Quarry, Kansas, *Platygonus* sp. ($N = 3$); MMCN 246, *P. chapadmalensis*, Prov. Buenos Aires. *Prosthennops*: *P. crassigenis*, Ainsworth area, Nebraska; *Prosthennops* sp., Mixon Bone Bed, Florida.



wagneri is crenulated, and the posterior mass consists of a series of at least three cusps. In *Catagonus* both diameters of the P_3 are larger than those of *Tayassu*, most *Prosthennops*, *Platygonus* sp. of Edson Quarry, *P. compressus* of Welsh and Cherokee Caves, *P. scagliae*, and *P. chapadmalensis* (MMCN 246). A second group of *Platygonus* and allies with large crania, from the Upper Pliocene and Lower Pleistocene, have large, broad P_3 's, with transverse diameters above the O.R.'s of *Catagonus*, while their anteroposterior diameters overlap the O.R.'s of the latter genus. The transverse diameters and, as it was used by Kraglievich (1959) to distinguish *Argyrohyus*, the ratios of transverse to anteroposterior diameters are contrasted between *Catagonus* and this second group: *Catagonus* sp. (MMCN 707), 8.9 and .63; *C. wagneri*, holotype, 9 and .66; *C. wagneri*, Paraguay, 8.8 (8.1-9.8; N = 19) and .69 (.62-.74; N = 24) vs. *Platygonus texanus*, 12.4 (11.3, 13.5, Meade 1945) and .85 (.82, .89); *Argyrohyus chapadmalensis*, 10.7 and .88 (Kraglievich, 1959); *Platygonus marplatensis*, 10.2 and .85 (ibid.); *Platygonus* sp. (MMCN 1212), 10.05 and .82. These same ratios for the first group of *Platygonus* ranged from .77 (*Platygonus* from Edson Quarry) and .78 (*P. compressus* from Welsh Cave, from \bar{Y} 's of Guilday et al., 1971) to .82 (*P. cumberlandensis* and *P. chapadmalensis*). The *Prosthennops* specimens (AMNH) differ by having very slender P_3 and low diameter ratios: *P. niobrarenensis*, .62 (.60, .65) and *P. crassigenis*, .61.

P_4 : The last permanent premolar of the genus *Catagonus* is molariform, nearly as large as the first molar, and has four major cusps. This is in contrast to *Platygonus*, which has much smaller P_4 's with only two major cusps (Figs. 3 and 4). In Paraguayan *C. wagneri* (Fig. 8) the anteroposterior length of the P_4 (\bar{Y} , 15.0; N = 36) exceeds that of even the large *Platygonus*, MMCN 1212 (11.4) of the Lower Pleistocene of Argentina, as well as the large Blancan species reported by Meade (1945:528), *P. bicalcaratus*

(11.0, 11.4, 12.0) and *P. texanus* (14.0). Although in *Tayassu* and the *Prosthennops* examined, the P_4 's are more molariform than in *Platygonus*, they do not have four equal major cusps nor do they attain anteroposterior diameter approaching that of the M^1 . In *Tayassu*, the P_4 has only three major cusps. If the supernumerary teeth in the holotype of *P. (Brasiliochoerus) stenocephalus* (Winge, 1906: Plate 6) are molars, the P_4 apparently has four cusps and approaches the length of the molar.

The greater size of the P_4 of *Catagonus* as compared to *Platygonus* and relatives is illustrated by the following series of anteroposterior diameters: *C. wagneri*, Paraguay, 16.2 (14.4-19.4; N = 22); *Platygonus texanus* (MU 6415), 14.5; *Platygonus* sp. (MMCN 1212), 14.2; *P. bicalcaratus* (TMM 31175-12), 13.9; *P. marplatensis*, 13.0 (Reig, 1952:122); *Argyrohyus chapadmalensis*, 12.5 (Kraglievich, 1959:226); *Platygonus cumberlandensis*, 12.2 (N = 4); *P. chapadmalensis* (MMCN 246), 10.8; *P. compressus*, Welsh Cave, 10.8. Although all the foregoing specimens had smaller anteroposterior diameters than *Catagonus*, some of them had transverse diameters approaching that genus. The ratios of transverse to anteroposterior diameter reflect this character, as pointed out by Kraglievich (1959) for *Argyrohyus*: *Catagonus bonaerensis*, .78; *C. rebuffoi*, .72; *C. wagneri*, Paraguay, .77, s = .04 (.66-.82; N = 25) vs. *Platygonus marplatensis*, 1.00 (Kraglievich, 1959); *P. cumberlandensis*, .97 (.94-1.00; N = 4); *P. chapadmalensis* (MMCN 246), .95; *Argyrohyus chapadmalensis*, .93 (Kraglievich, 1959); *Platygonus texanus* (MU 6415), .92; *P. bicalcaratus* (TMM 31178-13), .91.

M^1 : The anterior and posterior cingula are interrupted at mid-point by cusps. A variable number of three to four cusps lie between these anterior and posterior cusps. As in the other maxillary cheek teeth, a cingulum on the buccal side is continuous with cingula of the anterior and posterior faces. Both diam-

◀ Fig. 8. Comparison of Recent and fossil peccaries; lines and bars as in Fig. 7. Measurements are from this study and from the literature as follows: *Catagonus*: A, *C. metropolitanus* and B, *C. bonaerensis*, holotypes, Prov. Buenos Aires, Mid-Pleistocene (Rusconi 1930); C, *C. wagneri*, holotype and topotype, Prov. Santiago del Estero, pre-Hispanic (Rusconi 1948); D, *C. carlesi*, holotype, Prov. Santiago del Estero, Mid-Pleistocene (Rusconi 1930); Chaco, *C. wagneri*, Paraguay, Recent (N=36). *Platygonus*, reading from top down: MHN 313, *Platygonus* sp., Caves of Minas Gerais, Pleistocene; Edson Quarry, Kansas, *Platygonus* sp., Upper Pliocene (N=5); Cumberland Cave, Maryland, *P. cumberlandensis*, holotype and paratypes, Mid-Pleistocene (N=5); Blanco Beds, Texas, *P. bicalcaratus*, Blancan (Meade 1945); MMCN 1212, *Platygonus* sp., Prov. Buenos Aires, Lower Pleistocene; MHN 305, *Platygonus* sp., Caves of Minas Gerais, Pleistocene; Cherokee Cave, Missouri, *P. compressus*, Upper Pleistocene (Simpson 1949); Welsh Cave, Kentucky, *P. compressus*, Upper Pleistocene (Guilday et al. 1971); MMCN 246, *P. chapadmalensis*, Prov. Buenos Aires, Lower Pleistocene; *P. scagliae*, holotype, MMCN 156, Prov. Buenos Aires, Lower Pleistocene. *Tayassu*: *T. pecari*, Paraguay, Recent (N=22); *T. tajacu*, Paraguay, Recent (N=18).

eters of the first upper molars of *Catagonus* are larger than those of *Tayassu*, *Platygonus compressus*, and *P. scagliae*. The transverse diameter of *Catagonus* is greater than that of *P. bicalcaratus* (MU 6415) and *P. chapadmalensis* (MMCN 246), but smaller than that of *P. texanus* (TMM 31175-12).

M₁: Cuspules occur near the midlines of the anterior and posterior cingula. Medial cuspules lie in the valley between the anterior and posterior pairs of major cusps. Unlike the M₁ of *Tayassu* and *Platygonus*, there is a definite cuspule on the lingual side of the valley between the two pairs of major cusps. In unworn M₁ this is flanked by a lesser cuspule in the buccal position. The anteroposterior diameter of the M₁ of *Catagonus* is larger than that of *Tayassu* or *Platygonus*. The transverse diameter overlaps that of *P. texanus* (MU 6415), *P. bicalcaratus* (TMM 31178-13), *P. cumberlandensis*, and *Platygonus* sp. (MMCN 1212).

M₂: Pronounced cuspules occur medially at the anterior and posterior borders of the second upper molar. As with the M₁, medial cuspules lie next to the valley between the two moieties. Cingula bind the buccal and, except for the interruption by cuspules, the anterior and posterior margins of the tooth. Both diameters of the M₂ of *C. wagneri* are larger than in *Tayassu*, *P. compressus*, *P. scagliae*, and *P. chapadmalensis* (MMCN 246). The O.R.'s overlap those of *P. texanus* (MU 6415), *P. bicalcaratus* (TMM 31175-12), *P. cumberlandensis*, and *Platygonus* sp. (MMCN 1212). The entire sample is dwarfed by the transverse diameters of *P. henningi* Rusconi (1930), 21.3; and *Catagonus* sp. (MMCN 707), 22.6.

M₂: The second lower molar is similar to M₁ except that it is larger in all dimensions and has more pronounced cuspules. In *Catagonus*, both diameters of this tooth are greater than those of *Tayassu*, *P. compressus*, *P. chapadmalensis* (MMCN 246), *P. scagliae*, and *Prosthennops*. The O.R.'s of both dimensions overlap those of *P. cumberlandensis*, *P. texanus* (MU 6415, 6416) and *P. bicalcaratus* (TMM 31178-13, 31197-2). Transverse diameter of the M₂ in the large *Platygonus* specimen (MMCN 1212) is 19.8, and that of *Catagonus* sp. (MMCN 707), 20.6 as compared to *C. wagneri*, $\bar{Y} = 16.5$ (O.R., 15.1-17.8; N = 27).

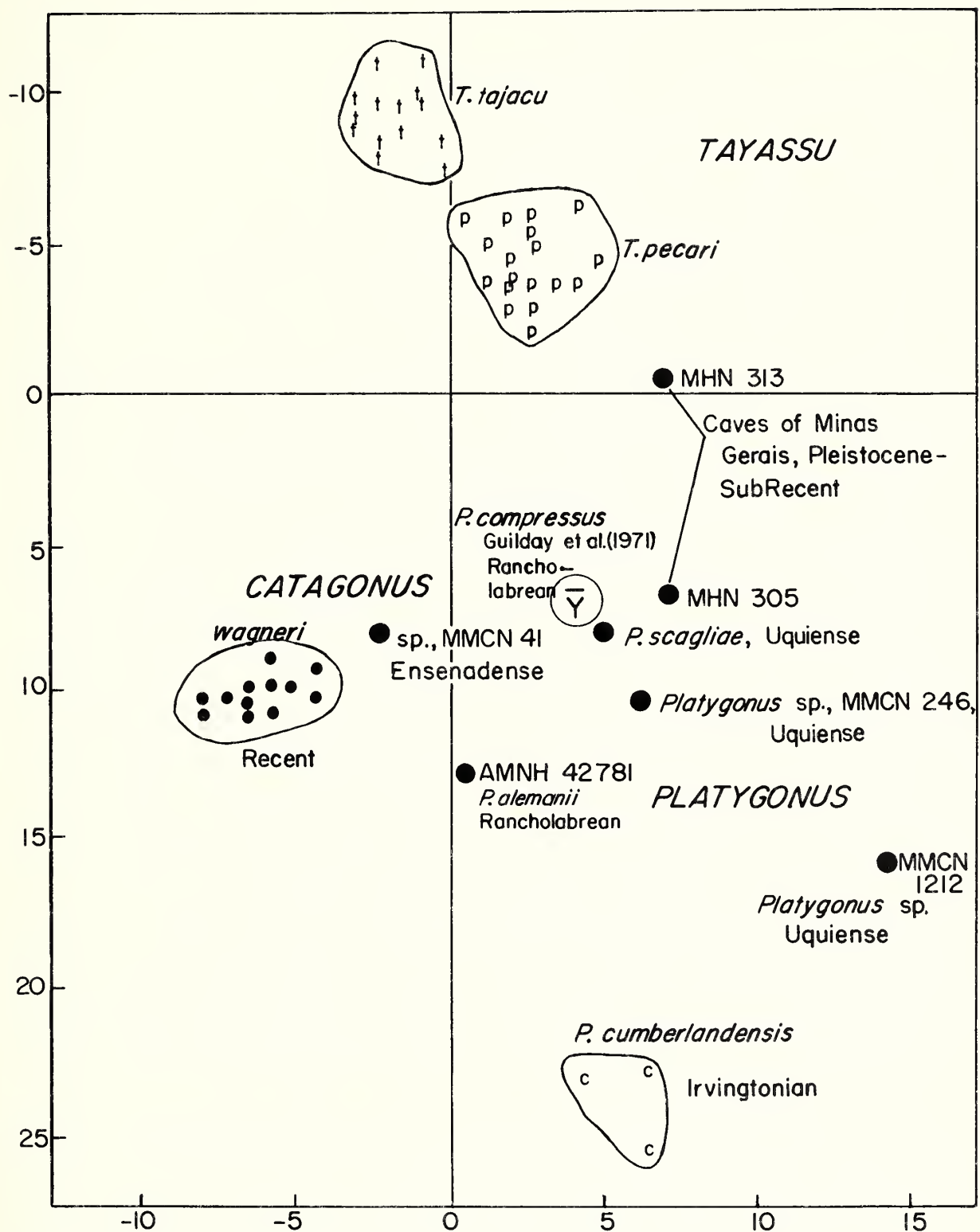
M₃: The last upper molar of *Catagonus* is quadrangular in outline, lacking the distinct posterior constriction in transverse width that occurs in *Tayassu*, *Mylohyus*, and most *Platygonus* and *Prosthennops*. Figures 3 and 4 show the four major cusps, the cuspules, and truncated appearance of the M₃. Some ratios of greatest transverse diameter of the posterior moiety to anterior moiety follow: *C. wagneri*, Paraguay, .92, s = .03 (O.R., .87-.96; N = 14); *Catagonus* sp. (MMCN 41), Mid-Pleistocene, Argentina, .96; *Platygonus bicalcaratus* (TMM 31175-12), Blancan, .89; *P. scagliae*, holotype, Lower Pleistocene, Argentina, .88; *P. compressus*, Upper Pleistocene, Missouri, .85 (Simpson 1949:29; ratio of means of W_p to W_a); *P. cumberlandensis*, Mid-Pleistocene, Maryland, .88 (.79-.96; N = 3); *Prosthennops crassigenis*, late Clarendonian, Nebraska, .86 (.81, .90); *P. edensis*, late Hemphillian, California, .93; *Prosthennops* sp., late Hemphillian, Florida, .86; *Tayassu tajacu*, Recent, Paraguay, .88 (.86-.95; N = 4); *T. pecari*, Recent, Paraguay, .88 (.82-.97; N = 9).

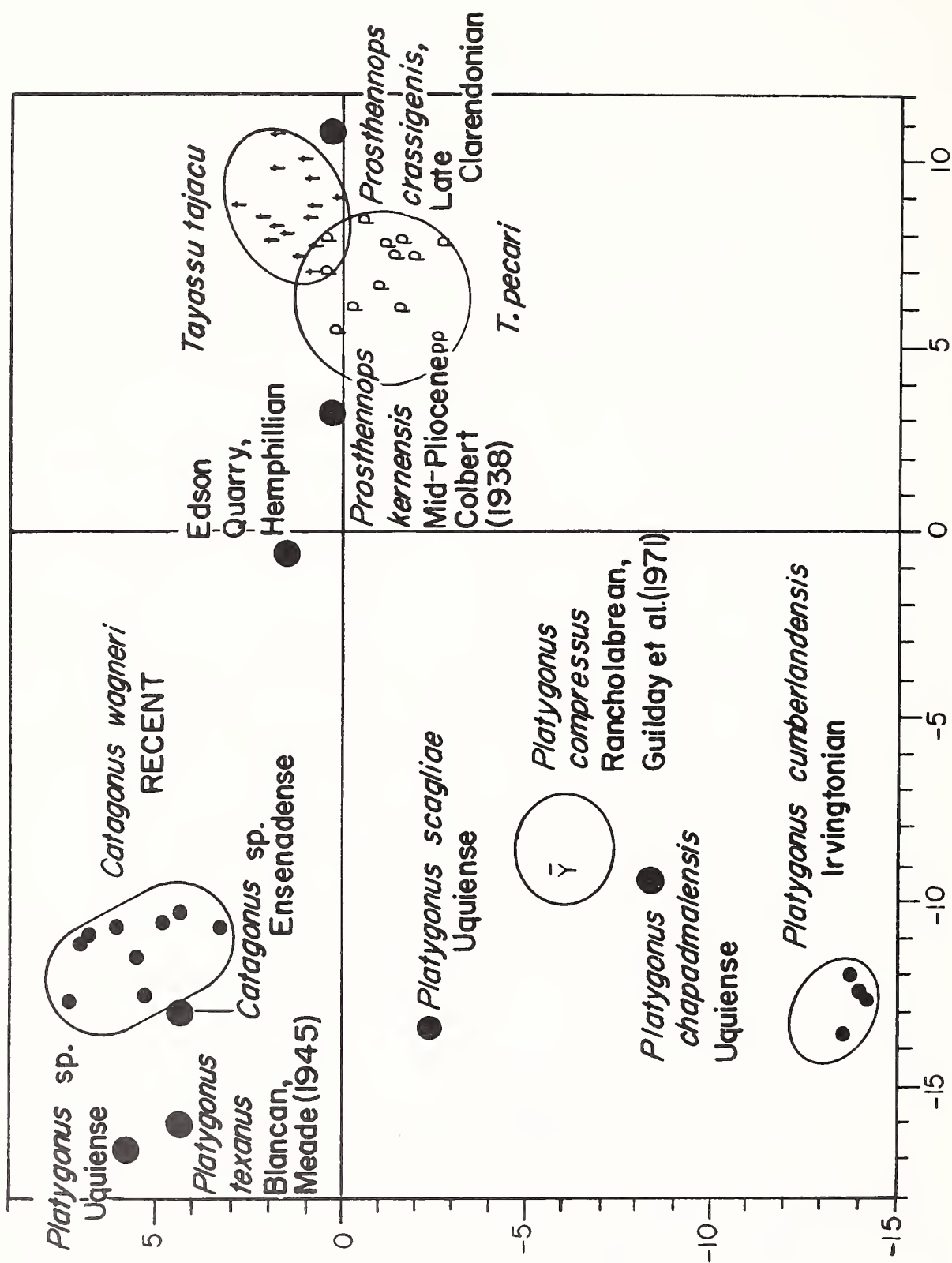
The appearance of posterior taper is accentuated in *Mylohyus*, *Tayassu*, and most *Platygonus* by the presence of a posterior lobe or heel as contrasted with the truncated M₃ of *Catagonus*, *Prosthennops*, and *Platygonus bicalcaratus*. The M₃'s of *Catagonus* and *P. bicalcaratus* (TMM 31175-12)¹ are quite similar, both having a well-developed cingulum on the posterior margin. The chief differences in *C. wagneri* are the less pronounced posterior taper and the presence of medial cuspules, including one dividing the posterior cingulum rather than the medial ridge that divides this cingulum in *P. bicalcaratus*.

Both diameters of the M₃ of *C. wagneri* are larger than those of *Tayassu*, *Platygonus compressus*, *P. scagliae*, *P. chapadmalensis*, *Platygonus* spp. (MHN 305, 313), and *Prosthennops crassigenis*. The O.R.'s

¹Hibbard and Riggs (1949, Bull. Geol. Soc. Amer., 60:829-860), followed by Dalquest (1975, Occ. Papers No. 30, The Museum, Texas Tech Univ.), considered *P. texanus* to be conspecific with *P. bicalcaratus*. It is convenient for discussion purposes here to retain the two species, following Meade (1945), rather than speak of "texanus-like *P. bicalcaratus*" with a distinct heel on the M₃ (MU 6415) and "typical *P. bicalcaratus*" with a truncated M₃ (TMM 31175-12).

Fig. 9. Canonical analyses, fossil and Recent peccaries, 21 variables as follows: condylobasal length, rostral length, greatest width across maxillary toothrow, palatal widths inside P₂'s and M₂'s, height of cranium at condyles, length of postcanine diastema, length of P₂-M₃, length of P₂-4, length of M₁-3, and anteroposterior and transverse diameters of individual maxillary teeth from P₃ to M₃. Except for *P. compressus*, Welsh Cave (Guilday et al. 1971), measurements are from this study. Note: *Platygonus* sp., MMCN 246 = *P. chapadmalensis*.





of the anteroposterior diameter overlap that of *Prosthennops edensis*, *Prosthennops* sp. from Mixon Bone Beds *Platygonus* spp. (MMCN 1212, MHN 309), *P. bicalcaratus*, and *P. marplatensis*. The M^3 of *C. wagneri* is much smaller in both dimensions than *Catagonus* sp. (MMCN 707), in transverse diameter than *P. bicalcaratus* and *P. marplatensis*, and in anteroposterior diameter than *P. texanus* (MU 6415).

M_3 : The last lower molar differs from the truncated upper molar in having a large, median posterior cusp. This cusp (hypoconulid) in *Catagonus*, as well as in *Platygonus*, has an undivided point and is a prominent feature of the M_3 , secondary in height only to the pair of major cusps in each moiety. The equivalent posterior lobe in *Tayassu* is highly variable, with numerous cuspules. In *Catagonus*, a cuspule lies on the buccal flank of the posterior cusp. The cingulum on the anterior face of the M_3 is interrupted by a median cuspule and the overlapping posterior cuspule of the M_2 . A chain of medial cuspules extends from the

valley between the anterior pair of major cusps to the large posterior cusp.

The transverse diameters of the posterior and anterior moieties of M_3 in *C. wagneri* are nearly equal (Fig. 4), as compared with proportionally lesser widths of the posterior moiety in other specimens examined. This greater posterior taper is illustrated by the following ratios of transverse diameter of posterior moiety to anterior moiety: *C. wagneri*, Recent, Paraguay, .98 (O.R., .95-1.0; $N = 10$); *Platygonus compressus*, Rancholabrean, Missouri, .96 (Simpson, 1949:30; ratio of means of W_p to W_a); *P. cumberlandensis*, Irvingtonian, Maryland, .86; *P. bicalcaratus*, Blancan, .91 ($N = 2$); *P. texanus*, Blancan, .90; *P. marplatensis*, holotype, .89; *Prosthennops* sp., late Hemphillian, Florida, .90; *P. crassigenis*, late Clarendonian, Nebraska, .86; *P. niobrarensis*, Valentinian, Nebraska, .79; *Tayassu pecari*, Recent, Paraguay, .89 (.84-.94; $N = 10$); *T. tajacu*, Recent, Paraguay, .91 (.84-.97; $N = 10$).

DISCUSSION AND CONCLUSIONS

The close relationship of the genera *Catagonus* and *Platygonus* indicated in the foregoing comparisons is also supported by canonical analyses. Multivariate comparisons were made using width and length of mandibular teeth plus length of mandibular diastemas, maxillary teeth measurements, and all the measurements or combinations listed for Figures 9 and 10. In Figure 9, the specimens of *Catagonus* are positioned adjacent to the middle of the grouping of *Platygonus* specimens from the Pleistocene of both South and North America. This is also shown in Figure 10, except that the closeness of two large specimens of *Platygonus* to *Catagonus* is exaggerated. Some of the large dimensions of the teeth of *Platygonus* sp. (MMCN 1212) and *P. texanus* are similar to those of *Catagonus*, but when cranial dimensions are included in the multivariate comparisons, as in Figure 9, this relationship is not so close. Note also that in Figure 8 the dimensions of a single critical tooth, P^4 ,

of the Blancan specimens and MMCN 1212, are similar to each other and group with the rest of *Platygonus*, well separated from *Catagonus*.

The specimens of *Platygonus* from the South American Pleistocene, although separable from *Catagonus* by both multivariate and univariate comparisons, show some blending of *Platygonus* and *Catagonus* characters not noted in the North American *Platygonus*. *P. scagliae*, *P. chapadmalensis*, and *Platygonus* sp. (MMCN 1212), all from the Lower Pleistocene (Uquiense), have typical *Platygonus* P^4 (see Fig. 8), but show some similarity to *Catagonus* in cingula on the anterior and buccal sides of P^{2-4} and M^{2-3} . In the relationship of the maxillary postcanine diastema to length of M^{1-3} , *P. chapadmalensis* is also intermediate between *Catagonus* and *Platygonus* (see Fig. 7).

All multivariate comparisons, including those shown in Figures 9 and 10, positioned *Tayassu pecari* closely with *T. tajacu*. *Tayassu* is widely separated

◀ Fig. 10. Canonical analyses, fossil and Recent peccaries, 26 variables as follows: lengths P_3^2 - M_3^3 , P_{2-4} , M_{1-3} , anteroposterior and transverse diameters of individual teeth from P^3 to M^3 and P_2 to M_3 . Measurements from the literature are indicated in figure; measurements from this study are as follows: *Catagonus*: *C. wagneri*, Paraguay, Recent; *Catagonus* sp., MMCN 41, Prov. Buenos Aires, Mid-Pleistocene. *Platygonus*, reading from top down: *Platygonus* sp., MMCN 1212, Prov. Buenos Aires, Lower Pleistocene; *Platygonus* sp., Edson Quarry, Kansas, Upper Pliocene; *P. scagliae*, holotype, MMCN 156, Prov. Buenos Aires, Lower Pleistocene; *P. chapadmalensis*, MMCN 246, Prov. Buenos Aires, Lower Pleistocene; *P. cumberlandensis*, holotype and paratypes, Cumberland Cave, Maryland, Mid-Pleistocene. *Prosthennops*: *P. crassigenis*, Ash Hollow Formation, Florida, Lower Pliocene. *Tayassu*: *T. pecari* and *T. tajacu*, Paraguay, Recent.

from *Catagonus* in all these comparisons, but near some *Prosthennops* (Fig. 10) and two *Platygonus*, MHN 313 (Fig. 9) and MHN 305 (Table 5). The latter specimens are from caves in the region of Lagoa Santa, Minas Gerais. These and other MNH specimens strongly suggest a phylogenetic continuum from *Prosthennops*-*Platygonus* to modern *Tayassu pecari*. As none of the Lagoa Santa specimens at MNH have M²'s larger than M³'s, as does *Platygonus* (*Brasiliochoerus*) *stenocephalus* (see Table 3), I have not followed Paula Couto's (1970:7) application of that name to the large specimens in that collection.

Woodburne (1968:30-32) hypothesized that a common ancestor of *T. pecari*, *P. (Brasiliochoerus) stenocephalus*, and *Mylohyus* would be *Prosthennops niobrarensis* Colbert (Valentinian, Lower Pliocene of Nebraska). The additional specimens from Minas Gerais at MNH, not seen by Woodburne, suggest that *T. pecari* originated in South America, probably either in the forested highlands of Brazil or during a period of isolation in a forest center in the Amazonian basin. Woodburne also believed there was an affinity of *T. tajacu* with the *Platygonus compressus* group and considered the similarity of their common ancestry to certain peccaries in the Frick Collection (AMNH)—the specimens from Edson Quarry, Kansas (Woodburne, pers. commun.). In the present study some comparisons place these Edson Quarry specimens in the genus *Platygonus*. In other comparisons they fall in an intermediate position with *Platygonus*, *Catagonus*, and *Tayassu*, and seem to support Woodburne's idea, but with *T. pecari* and *T. tajacu* more closely related to each other than to any other species. It is probable that *T. tajacu* evolved in South America from a proto-*T. pecari*. Both the more northerly extension of the range of *T. tajacu* and its much smaller size, which would have made available to them many more suitable dens in which the species could take refuge, suggest that the selective force was cold stress upon a population isolated in montane forests. In tracing origins of *T. pecari* separate from *T. tajacu*, Woodburne placed chief emphasis upon difference in origin of two muscles of mastication, but ignored the many common characters in which they differ from other genera. I would not challenge his excellent list of salient differences (ibid.:28-29), except for the minor note that exceptions to his differences, numbers 9, 19, 22, 26, and 27, have been encountered in peccaries from Venezuela and Paraguay. And, of course, I would use his list of characters as specific rather than generic differences.

The early history of *Catagonus* cannot be traced with the data at hand, but its close relationship to *Platygonus* seems apparent. In many respects, *C. wagneri* is more conservative than *P. cumberlandensis* and *P. compressus* of the Middle to Upper Pleistocene—in retention of dewclaws on the forefeet and the third pair of lower incisors, in failure to develop the flaring zygomata, angular processes and orbits, the canine buttresses, and the symphyseal keel. In these features and in the more gracile skull, *C. wagneri* more nearly resembles *Platygonus* of the Upper Pliocene. Also, the molariform premolars of *C. wagneri* are somewhat like those of *Prosthennops* of the Pliocene.

The more primitive features of *C. wagneri* suggest that its ancestry was not subjected to as severe selection toward a specialized cursorial existence in open habitats as has been suggested for *Platygonus* by Guilday et al. (1971). North American *Platygonus* was preyed upon by large, cursorial carnivores that were absent in South American grasslands. This may have provided a selective force developing a more cursorial group in North America (Guilday, pers. commun.). Another effect of greater predation pressure upon North American *Platygonus* might have been the selection of males with larger canines for defense of the herd. *Catagonus*, not subjected to this degree of selective predator pressure upon defenders of the herd, would retain a more ancestral, minimal sexual dimorphism. In support of this thesis, the variation in size of canines and canine buttresses in *Platygonus* is greater by five-fold than in *C. wagneri*.

Despite its more conservative evolution, *C. wagneri* retains those features of *Platygonus* that are probably adaptive for a cursorial life in an open, arid habitat: Greater size than the other modern peccaries, elongated limbs, basicranial flexure associated with eye position and long rostrum, loss of some external dewclaws, and extreme development of olfactory chambers and sinuses.

The close relationship of *Catagonus* and *Platygonus* does not necessarily indicate a phylogenetic continuity: A better understanding of the limits of *Prosthennops* and *Platygonus* is needed. If the limit of the genus *Platygonus* is restricted by the presence of non-molariform premolars, *Platygonus* and *Catagonus* must be considered to be sister groups, with *Prosthennops* containing a common ancestor.

Catagonus wagneri has survived as a component of the Chaco dispersal center (as used by Müller, 1973) along with other mammalian species such as the three-

banded armadillo *Tolypeutes matacus*, the greater pichiciego *Burmeisteria retusa*, the cricetid rodent *Pseudoryzomys wavrini*, and the mara *Dolichotis salinicola*. The growing literature on climatic and biotic fluctuations in South America and their possible correlation with the glacial cycles of the world has been recently summarized by Müller (1973), Haffer (1974), and Short (1975). Little is known of the history of the Chaco in the Pleistocene except that it also was subjected to xeric-mesic cycles that extended into postglacial times (Short, 1975:171). It is possible that in the Chaco, *Catagonus* and other arid-adapted plants and animals were afforded suitable habitats that were continuous with other nonforest centers during aridity cycles. Müller found, for example, strong affinities between the Chaco and the Brazilian Caatinga centers. His Pampa center has more affinities with the Chaco center than he presents, an example being the range of one of his indicator species, the hairy armadillo *Chaetophractus villosus*. This species is not confined to the Pampa center as recorded by Cabrera (1958:214) but, as we have found in our studies in Paraguay, occupies the Chaco center as well.

Such a speculative picture of Pleistocene ebb and flow of *Catagonus* populations should be tempered with an accounting for the isolation of *C. wagneri* in a single zoogeographic center. Some features suggest that the Chacoan peccary, evolving from larger ancestors of the Pleistocene, has become stunted. The large skull vs. the proportionally smaller body and the large, crowded premolars and molars vs. the short diastema and graecile skull may seem to support this hypothesis. Although our knowledge of this newly dis-

covered living relict is presently inadequate for this task, it is tempting to invoke either, or both, genetic drift in a restricted population (an islandic type of speciation) or severe selection toward a smaller-bodied *Catagonus* in a minimally adequate habitat. It is reasonable to suppose that in an earlier, more mesic cycle, the habitat for *Catagonus* was much more restricted than now. It is also reasonable to consider that its habitat may have been a rather unsatisfactory compromise between minimally adequate temperature, when the pampean grasslands to the south were no longer warm enough for peccaries, and the nearest available semi-open habitat—the thorn scrub of the Chaco.

In conclusion, *Catagonus wagneri* is a diurnal, cursorial animal, better equipped for far vision and speed for escape from predators than are the nocturnal *Tayassu*. *C. wagneri* is also an “olfactory” animal, utilizing an elaborate sinus system as a dust trap in the semi-arid environment to which it is restricted. Both preliminary stomach analyses and tooth structure indicate that *C. wagneri* is a browser, as compared with the more omnivorous *Tayassu*. *T. pecari* and *T. tajacu* have survival advantages over *C. wagneri* in having larger brains, either actually or proportionally, probably greater flexibility of diet, and shorter rostra affording greater flexibility of head positions without interference with forward vision. The three species of living peccaries meet in the Gran Chaco during what may be an interim period—the present—between a more arid cycle that favored thorn forest, steppe, and *C. wagneri*, and a moist cycle that will increasingly favor more mesic forests and *Tayassu*.

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BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 4, pages 1-62, figures 1-28, tables 1-6

Issued 1 August 1978

Price: \$5.00 a copy

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CONTENTS

Abstract	5
Introduction	5
Abbreviations and Usage	5
Stratigraphic Distribution	6
Systematics	10
Subfamily Schizotheriinae	10
Included Genera	10
Known Distribution	10
Revised Diagnosis	10
Discussion	10
Genus <i>Moropus</i>	11
Included Species	11
Known Distribution	11
Diagnosis	11
Discussion	11
<i>Moropus elatus</i> Marsh	12
Lectotype	12
Paralectotype	12
Hypodigm	13
Diagnosis	13
Discussion	13
Description and Comments	13
<i>Moropus distans</i> Marsh	45
Lectotype	45
Paralectotype	45
Hypodigm	45
Diagnosis	47
Discussion	47
Description and Comments	47
<i>Moropus oregonensis</i> (Leidy)	48
Holotype	48
Hypodigm	48
Diagnosis	48
Discussion	48
Description and Comments	48
<i>Moropus hollandi</i> Peterson	49
Holotype	49
Hypodigm	49
Additional Material	49
Diagnosis	49
Discussion	50
Description and Comments	50
Conclusions and Zoogeography	59
Acknowledgments	60
Literature Cited	60

ABSTRACT

The subfamily Schizotheriinae, as represented by the genera *Schizotherium*, *Borissiakia*, *Moropus*, *Phyllostillon*, and *Ancylotherium*, is distinguished from the Chalicotheriinae by its more elongated, higher crowned molar teeth and less progressive foot structure. Of these genera, only *Moropus* ever reached North America, arriving in the medial or late Arikareean. Four late Arikareean/early Hemingfordian species of *Moropus* are recognized. *Moropus distans*, the type species, is represented by a few postcranial remains of small size. Based on comparison with other *Moropus* species, it is closely related to, and may be synonymous with, *Moropus oregonensis*, a species also from the late Arikareean of Oregon but represented only by dental remains. *Moropus elatus* and *Moropus hollandi* of the Great Plains

include individuals near the large end of *Moropus* size range and are more closely related to one another than either is to *M. distans* or *M. oregonensis*. *M. elatus* is quite well known from numerous individuals and is an important basis for studies of intraspecific variation and interspecific and intergeneric comparisons. *M. hollandi* is unique among *Moropus* species in having lost the trapezium from the manus. *Moropus senex*, represented by a single phalanx from Oregon, is considered a *nomen dubium*. *Moropus* is known to have ranged from Oregon to Florida in the late Arikareean and also occurs in the Aquitanian of France. Fragmentary, scattered remains are the worst barrier to an understanding of the early evolutionary history of this genus.

INTRODUCTION

Excavations by Carnegie Museum of Natural History expeditions at the Agate Spring Quarries in Sioux County, northwestern Nebraska, between 1904 and 1908 provided the major stimulus for the first comprehensive review of North American chalicotheres. In 1914, Holland and Peterson published a complete description of material of *Moropus elatus* collected by the Carnegie Museum of Natural History at Agate and included a comparison with known remains of *Moropus hollandi* and other species of *Moropus*. No broad rediscussion of *Moropus* has appeared since. In 1970, I began a restudy of the Schizotheriinae (Coombs, 1973), with

special emphasis on Hemingfordian and later North American relatives of *M. elatus*. This later material had been only peripherally studied by Holland and Peterson, and much new material had appeared. Some of the results of this study have been published (Coombs, 1974, 1975, 1976), but before a complete reevaluation of the later species will be meaningful, it is necessary to rediscuss the early Miocene North American species of *Moropus* using newer material and data. Planned functional and zoogeographic considerations of *Moropus* also necessitate this reevaluation.

ABBREVIATIONS AND USAGE

The following museum abbreviations are used with specimen numbers:

AM—Pratt Museum, Amherst College, Amherst;
AMNH—Department of Vertebrate Paleontology, American Museum of Natural History, New York;
CM—Carnegie Museum of Natural History, Pittsburgh;
F:AM—Frick American Mammals, American Museum of Natural History, New York;
FMNH—Field Museum of Natural History, Chicago;
UCMP—University of California, Museum of Paleontology, Berkeley;
YPM—Peabody Museum of Natural History, Yale University, New Haven.

Other abbreviations used are Mc and Mt followed by a Roman numeral to indicate, respectively, metacarpal and metatarsal.

The anatomical terms generally follow usage by Butler (1965), except where an element was not discussed by him; the terminology utilized by Holland and Peterson (1914) is often obsolete. Directional terminology applied to the skeleton is as follows:

- A. Dorsal-ventral as applied to the skull, vertebrae, and pelvis;
- B. Anterior-posterior as applied to skull (including tooth-rows), vertebrae, pelvis, scapula, and long bones of fore and hind limbs;
- C. Dorsal-volar (=anterior-posterior, dorsal-ventral, dorsal-plantar of several other authors) for carpals, metacarpals, tarsals, metatarsals, and phalanges;
- D. Radial-ulnar (=medial-lateral) for carpals, metacarpals, and phalanges of the manus;
- E. Tibial-fibular (=medial-lateral) for tarsals, metatarsals, and phalanges of the pes; and
- F. Labial-lingual in reference to the teeth.

The three phalanges of each digit are named, respectively, proximal, medial, and ungual (the latter is the fissured claw); this designation is to avoid the confusion with digit numbers (I–V), which results when the phalanges are also given numbers. Fused proximal and medial phalanges of digit II of the manus and occasionally also of digit II of the pes are termed duplexes following the usage of Holland and Peterson (1914).

STRATIGRAPHIC DISTRIBUTION

Skinner's report (1968) correlating chalicotheriid occurrences in North America provided an important basis on which the present study could build. Nevertheless, new chalicothere finds, discovery of additional specimens in old collections, further data concerning the location or correlation of old localities, and the greater knowledge acquired through further taxonomic study all make necessary a re-discussion of stratigraphic distribution. A map of the localities discussed is provided in Fig. 1. Localities yielding chalicotheres of medial Hemingfordian or later age and of uncertain age will be discussed in later papers. Although chalicothere remains can give some idea of the correlation of deposits, they are usually too rare and too incomplete to be of much practical value in biostratigraphy.

John Day Formation.—Skinner (1968:12–13) suggested that *Moropus distans* and *M. senex*, species established by Marsh from the John Day Basin, could be from the Rattlesnake Formation or Mascall Formation in the region, as well as from the John Day Formation. Some additional data, which suggest that at least some of Marsh's material is from the John Day Formation, are available.

Specimen labels on *Moropus* material from the John Day Basin give the following general locality information: 1) YPM 12193a, holotype of *Moropus distans*—"Bridge Creek beds" (Marsh specimens included in the hypodigm have the same collecting data); 2) YPM 12194, holotype of *M. senex*—"Dayville?, Oregon"; 3) YPM 10030, holotype of *M. oregonensis*—"Upper John Day beds, Bridge Creek, Wasco County, Oregon," collected by Condon (additional specimens from the same locality catalogued as YPM 10030a, 10030b); 4) AMNH 7259, referred by Holland and Peterson (1914) to *M. oregonensis*—"near Antelope Springs, Oregon." Although none of this data is precise enough to suggest exact locations, at least the "Bridge Creek beds" included important early collecting areas in the John Day Formation. The size and morphology of the specimens is near that hypothesized for early Miocene *Moropus* immigrants to North America and may suggest a relatively early age for the John Day chalicotheres. However, the designation of "Upper John Day beds" for the holotype of *M. oregonensis* signifies no more than that the specimen probably came from the John Day Formation. As Hay (1963), Rensberger (1971, 1973), and Fisher

and Rensberger (1972) have pointed out, the boundaries as designated by Merriam (1901) between members of the formation are not synchronous everywhere in the area. Fisher and Rensberger (1972) recently advocated a four-fold division of the John Day Formation; the divisions between members cross biostratigraphic boundaries, especially the division between the Turtle Cove Member and Kimberly Member. Fisher and Rensberger (1972:9) also pointed out the difficulties of using adherent matrix as a criterion for assigning formerly collected museum specimens to members of the John Day Formation.

Further information concerning distribution of chalicothere remains in the John Day Formation may be forthcoming. In the John Day stratigraphic collection being studied by Rensberger is a small chalicothere phalanx. Rensberger, who intends to describe the occurrence along with the remainder of his perissodactyl collection, stated (personal communication, 1972) that the specimen came from a stratigraphic level, which represents an early or possibly medial Arikareean age. Although some of the earlier collected *Moropus* material from the John Day Basin may be younger than this, John Day chalicotheres are clearly among the earliest known representatives of *Moropus* in North America.

Harrison Formation and Upper Harrison Formation (=Marsland Formation sensu McKenna, 1965), *Nebraska and Wyoming.*—The highest frequency of *Moropus* specimens, including material of both *M. elatus* and *M. hollandi*, occurs in these two formations. Recently, Robert M. Hunt of the University of Nebraska has restudied the type areas of both formations and traced the contact between them to important fossil localities. One of the most far-reaching results of his study has been the conclusion that the Harrison-Upper Harrison contact lies below the Agate Spring Quarries and that therefore the well-known fossil assemblage from these quarries comes from the Upper Harrison Formation (Hunt, personal communication, 1976). By Hunt's reinterpretation, the fauna associated with the Harrison Formation is relatively sparsely known, but it does include isolated specimens of chalicotheres probably referable to *M. elatus*. Chalicotheres from the Agate Spring Quarries are in the present paper attributed to the Upper Harrison Formation, in accordance with Hunt's findings.



Fig. 1.—Map of Arikarean-early Hemingfordian *Moropus* localities discussed in this paper: 1) Caliente Formation, California; 2) Dayville, Oregon (type of "*M. senex*"); 3) Bridge Creek, near Mitchell, Oregon (types of *M. distans* and *M. oregonensis*); 4) near Antelope Springs, Oregon; 5) Lemhi River Valley, 46 mi southeast of Salmon, Idaho; 6) 7 mi south of Chugwater, Platte Co., Wyoming; 7) Big Muddy Creek, Wyoming; 8) Jay Em, Goshen Co., Wyoming; 9) near Van Tassell, Niobrara Co., Wyoming; 10) western Sioux County along Niobrara River, Nebraska (type of *M. hollandi*); 11) Agate Spring Quarries and American Museum-Cook Quarry, Sioux Co., Nebraska; 12) Morava Ranch Quarry and surrounding area, Box Butte Co., Nebraska (type of *M. elatus*?); 13) Buda local fauna, Alachua Co., Florida.

One important problem in discussions of *Moropus elatus* Marsh has concerned the geographic and stratigraphic position of its type locality in relation to strata exposed in the Agate Spring Quarries. Skinner (1968, Table 1, footnote a) correctly stated that Marsh's type of *M. elatus*, if from the locality suggested by Holland and Peterson (1914:226), could have come from one of several formations exposed near the mouth of Whistle Creek in Sioux County, Nebraska. However, Matthew (1929:520, footnote 1) had differed from Holland and Peterson's estimation of the locality in concluding that the type of *M. elatus* was actually found some 18 mi east of Agate, Nebraska, a site well east of that proposed by Holland and Peterson.

Matthew's reason for proposing that the type locality of *Moropus elatus* was farther east was based on some surface exploration and digging conducted

by Harold J. Cook and communicated by letter to Osborn in 1917 and 1918 and to Matthew in 1927. Cook had concluded that the Agate Quarry vicinity was too distant to have been easily visited from the stage road presumed to have been followed by Marsh's collector Hank Clifford en route between Sidney, Nebraska, and the Red Cloud Agency. Cook had discovered a fossil pocket, which appeared to have been previously worked, relatively close to the stage road and about 18 mi east of Agate. Cook collected at this spot some chalicotheres material, which he sent to the American Museum for study. Subsequently the specimens were examined by Richard S. Lull and compared with the type material of *M. elatus* at Yale University. Lull concluded (personal communication to Osborn, 1917) that Cook's material was similar in color, preservation, and general appearance to the type.

although no actual break contacts could be found. Unfortunately, I have been unable to locate Cook's specimens for further comparison.

Cook asserted (letter, 1927, quoted in Matthew, 1929:520, footnote 1) that the pocket in which he found the bones "is located in the lower part of the Upper Harrison beds, whereas the Agate Springs Fossil Quarries and the *Moropus* obtained there are some sixty feet below the top of the Lower Harrison beds." On this basis Matthew (same footnote) stated that the Upper Harrison species *M. hollandi* was probably synonymous with *M. elatus* and that the Agate Quarry material should be referable to a different species, *M. cooki* Barbour. Such a conclusion is not, however, borne out by specimen morphology.

Since Cook's excavation and possible discovery of Clifford's locality, the area between 16 and 20 mi east of Agate along the Niobrara River has been studied by parties of the Frick Laboratory and of the University of Nebraska. The area is complexly channeled and several formations are represented, including the type section of the Runningwater Formation (Cook, 1965). Cook's description of his old diggings stated, "It is really the nearest commanding hill to that old road crossing [Niobrara crossing], so it seems a particularly probable place for him [Clifford] to have found the type specimens [of *Moropus elatus*] figured and described by Marsh" (letter of 21 November 1917, to Osborn, bracketed material mine). Cook described the matrix as "mostly very hard around the bones, so that collecting is rather slow As the slope is largely grassed over, it is small wonder that bones at this spot should have missed recent attention by people living around there The color of the matrix varies a good deal locally, and the deposits are quite 'pockety,' due to channel beds, and shifting stream depositions" (H. J. Cook, letter to Osborn, 20 December 1917). These descriptions coincide very closely with the location and lithology of Morava Ranch Quarry, so it seems likely that Cook's locality was at or very near the site of the later quarry, excavated by Ted Galusha in 1940 and by me in 1975. It may also be at or near the original Clifford locality. *Moropus* remains from Morava Ranch Quarry agree quite well in color (bluish gray) and preservation with the type material of *M. elatus*. Detailed location of the Morava Ranch Quarry is available in Frick-American Museum records. As mapped in Cook (1965:3), it lies in a Harrison Formation channel, but this assessment may require

reevaluation as study of the area progresses. Morphologic evidence (below) suggests that Agate and Morava Ranch Quarry *Moropus* are referable to *M. elatus* and that *Moropus hollandi* is a separate but closely related species.

The Cook Collection at the American Museum of Natural History contains a number of chalicotheres remains, primarily teeth and foot elements, from the Agate Quarries and from north and east of Agate. Locality data for some of this material is not sufficient for placement in the Harrison or Upper Harrison Formation. Some material is from the American Museum-Cook Quarry, 2 mi north of the Agate Quarries. This latter locality was discussed in detail by Hunt (1972:35-37) and on the basis of data presented by him is almost certainly the place where American Museum parties collected an excellent skull, AMNH 10,645, referred to *M. elatus*. Hunt (personal communication, 1976) now places the American Museum-Cook Quarry in the base of the Upper Harrison Formation.

AMNH 13,765, an upper jaw with P³-M³ was collected by Olcott in 1907 at the "top [of] Lower Harrison beds, Van Tassel, Wyoming" (specimen field label by Olcott). This specimen yields very little information of specific taxonomic value and is regarded here as *Moropus* indet. Locality data are not precise enough to be certain that it comes from the Harrison Formation.

A thick section of the Upper Harrison Formation is exposed along the Niobrara River near the Nebraska-Wyoming state line. It was here that Peterson (1907a, 1909) designated the type section of the Upper Harrison beds. McKenna (1965) considered Peterson's section to be the type section of the Marsland Formation and used "the term Marsland [proposed by Schultz, 1938] as an objective synonym (at the rank of a formation) of the term Upper Harrison beds" (1965:10, bracketed material mine). In the Upper Harrison faunal list from this area, Peterson (1907a:56) included *Moropus ?elatus* Marsh, later in the paper (1907a:60) identified as CM 1424, found "near the base of the Upper Harrison beds on the Niobrara in Sioux County, Nebraska, in 1901." Peterson later (1913) made this specimen the type of a new species, *M. hollandi*. Holland and Peterson (1914:232) further specified the locality as "near Wyoming state line," and the Carnegie Museum catalogue lists further, "near Vantassel." No additional locality data is available. Hunt (personal communication) has found additional *Moropus* material at Harper Quarry, just above

the Harrison-Upper Harrison contact near the state line.

Additionally, Skinner (1968) mentioned deposits yielding chalicotheres from the Jay Em district, Goshen County, east-central Wyoming, and from 7 mi south of Chugwater, Platte County, south-eastern Wyoming. He considered them biostratigraphically equivalent to the Upper Harrison. Further, Riggs collected *Moropus* material, now at the Field Museum of Natural History, from beds presumably also Upper Harrison equivalents near Jay Em, Wyoming. Where diagnostic specimens are present, the Jay Em and Chugwater chalicotheres seem to be referable to *M. hollandi*. It is not presently clear to what extent the difference between *M. elatus* and *M. hollandi* represents an age and/or ecologic distinction between the faunas containing each. Correspondingly, the boundary between Arikareean and Hemingfordian *Moropus*-containing faunas needs redefinition.

Other Arikareean or early Hemingfordian occurrences.—Among the specimens collected by Amherst College expeditions of 1907–1908 at Big Muddy Creek, Wyoming, were several chalicothere phalanges. Locality and stratigraphic data with the material are inexact, and the Amherst College catalogue lists Muddy Creek specimens from “Lower Rosebud,” “Lower Harrison,” and “Upper Harrison” beds. The basis on which these distinctions were made is unclear. Loomis (1909, 1911) published on turtles and camels from Muddy Creek and concluded that they were from “Upper Harrison beds.” The type of *Testudo brevisterna*, he stated, was found near a skeleton of *Merychys minimus* and was thought to be “Upper Harrison” on that basis (Loomis, 1911). However, Schultz and Falkenbach (1947) mentioned no representatives of *Merychys* from Muddy Creek; they later (1949) listed the Monroe Creek genera *Mesoreodon* and *Merycoides* from Muddy Creek. McKenna and Love (1972) reevaluated *Oxydactylus gibbi* and *Protomeryx leonardi*, camel species named by Loomis (1911) from Muddy Creek. They referred both species to *Miotylopus gibbi* (Loomis) and considered it probable that the type specimens came from beneath the Harrison Formation. The Muddy Creek area and Yale and Amherst College collections derived from it need serious restudy. Monroe Creek equivalent beds clearly seem to be represented, but

Upper Harrison equivalents may be present also. The chalicothere phalanges from Muddy Creek are generally similar to and within the size range of Agate Quarry *Moropus elatus*. They are probably not useful for correlation, but they may be among the earliest known chalicotheriids in North America.

Patton (1967:8) mentioned the presence of a chalicothere in the Buda local fauna, near Newberry, Alachua County, Florida. Skinner (1968) gave a personal communication from Patton, which further identified the remains, whereas Patton and Webb (1970) described it as a “dwarf version of the large chalicothere . . . common in western faunas.” Patton and Taylor (1971:128) considered the fauna to be earliest Hemingfordian, but Rich and Patton (1975:695) subsequently suggested an Arikareean age. Patton intends to discuss the chalicothere at a future date. It should be noted in regard to the Buda specimen that specimens of small chalicotheres are also known from the John Day Formation in Oregon.

Repenning and Vedder (1961:C-237) reported a chalicotheriid in an Arikareean assemblage from continental deposits in the Caliente Formation of the eastern Caliente Range, California, between their sections 2 and 3 (1961:C-236) and about 3,000 ft above the base of their section. Repenning (personal communication) identified the remains as the proximal one-half of a rather small duplex bone (fused proximal and median phalanges), abraded and badly gnawed by rodents, and a ?chalicothere tooth fragment. Listed in the same fauna (1961:C-237) were *Oxydactylus brachyodontus* [?=*Paratylopus cameloides* (Wortman)] and *Parablastomeryx* aff. *P. falkenbachii* Frick, both restricted elsewhere to the late Arikareean and early Hemingfordian. Geology of this area has recently been detailed by Woodburne (1975).

Skinner (1968:18) mentioned a *Moropus* phalanx, F:AM 54,900, collected at the upper end of the Lemhi River Valley, about 46 mi southeast of the town of Salmon, Idaho. The age of the deposits was unknown but considered possibly biostratigraphically equivalent to the Marsland Formation (*sensu* McKenna, 1965) of the Great Plains. Morphology of the phalanx is not useful taxonomically and does not contribute any further information to a correlation.

SYSTEMATICS

Class Mammalia
 Order Perissodactyla
 Superfamily Chalicotherioidea Gill, 1872
 Family Chalicotheriidae Gill, 1872
 Subfamily Schizotheriinae Holland and
 Peterson, 1914

INCLUDED GENERA

Schizotherium Gervais, 1876; *Ancylotherium*
 Gaudry, 1862; *Moropus* Marsh, 1877; *Phyllotillon*
 Pilgrim, 1910; and *Borrissiakia* Butler, 1965.

KNOWN DISTRIBUTION

Oligocene-Miocene of Eurasia, Miocene of North
 America, Pleistocene of Africa (usage of Miocene
 as in Berggren and Van Couvering, 1974).

REVISED DIAGNOSIS

Dental formula I 0/1-3, C 0/0, P 3/3, M 3/3 (an-
 terior dentition not verified in all genera; see
 Coombs, in press); molar teeth higher crowned than
 in the Chalicotheriinae, with molars slightly to
 strongly elongated; protoloph on upper molars com-
 plete on unworn teeth; ectoloph on upper molars
 less strongly slanted than in the Chalicotheriinae
 (paracone and metacone in labial half of tooth);
 metastylid always separate from metaconid on low-
 er molars; jaw symphysis typically shorter and di-
 astema relatively longer than in the Chalicotheri-
 inae; Mt III longest metatarsal or Mt III and Mt IV
 subequal in length; Mc III longest metacarpal; fore-
 limbs versus hindlimbs not so disproportionate in
 length as in the Chalicotheriinae; proximal pha-
 langes more symmetrical than in the Chalicotheri-
 inae and ungual phalanges less transversely com-
 pressed.

DISCUSSION

The present-day classification of the Chalicotherioidea, which gives the early (primarily Eocene) chalicotheres (=Eomoropidae) equal rank with the later, unmistakably clawed group (=Chalicotheriidae), originated with Matthew (1929). Within the latter group he distinguished lineages having high-crowned and low-crowned molar teeth, now designated the Schizotheriinae and Chalicotheriinae. He did not, however, name his subgroups or give full family status to the Eomoropidae and Chalicotheriidae. These refinements evolved gradually in the works of later authors.

The accepted subfamilies Chalicotheriinae and

Schizotheriinae show better than any other simple taxonomic scheme the evolutionary relationships within the Chalicotheriidae. Particularly, they express the strong morphological and ecological divergence of *Chalicotherium* and closely related *Nestoritherium* from the remainder of the Chalicotheriidae. These Chalicotheriinae, while remaining generally conservative in their dental evolution, attained the most specialized limb structure, evident in even the earliest known representatives (*Chalicotherium pilgrimi*, *C. rusingense*). Among these unusual limb features are hindlimbs much shorter than forelimbs, loss of trapezium and Mc V, lunate displaced almost entirely onto the magnum, increase in length from Mc II through Mc IV and from Mt II through Mt IV, astragalus articulating with both navicular and cuboid, asymmetrical proximal phalanges with metapodial facet parallel to dorsal surface, and ungual phalanges strongly compressed transversely. Improved knowledge of the Chalicotheriinae is available in Butler (1965) and Schaefer and Zapfe (1971). Schizotheriines remain more conservatively perissodactyl-like in their foot structure but evolve more rapidly in their dentitions by increasing the crown height and length of molars, probably as a selective response to coarser diet. Schizotheriines are often associated with savannah faunas, whereas Chalicotheriinae are more often found with dense woodland assemblages.

Problems exist, however, in making a clear distinction between Chalicotheriinae and Schizotheriinae. Relations of the primitive Oligocene schizotheriine genus *Schizotherium* to the Chalicotheriinae are unclear. *Schizotherium* lacks the foot specializations of chalicotheriines, but its molars are not so elongated or high crowned as in other schizotheriines, although several species trend in this direction. More complete knowledge of *Schizotherium* should settle some of these questions. Another small difficulty arises because certain schizotheriines parallel the Chalicotheriinae in a few aspects of foot structure, although no schizotheriine attains the derived state seen in even the most primitive known chalicotheriines. Several schizotheriine species independently lost the trapezium; some *Ancylotherium* lost Mc V; the tall astragalus of *Borrissiakia* articulated with the cuboid as well as with the navicular; metatarsal length was gradually reduced in schizotheriine evolution (see Coombs, 1974). On the other hand, a few primitive species of *Chali-*

cotherium have a metastylid on lower molars, whereas most other chalicotheriines have a small metastylid or none. Parallelism and problematic primitive genera and species are not uncommon phenomena in taxonomic work, however, and in this case provide no special barrier to the acceptance of two chalicotheriid subfamilies.

The Chalicotheriidae made its first known appearance in North America during the Arikareean Land Mammal Age. Only the Schizotheriinae ever appeared in North America. All North American chalicotheriids could have been derived from a single or several Arikareean immigrants belonging to the genus *Moropus*.

Genus *Moropus* Marsh

Moropus Marsh, 1877:249.

Type species.—*Moropus distans* Marsh, 1877.

INCLUDED SPECIES

Moropus distans; *M. oregonensis* (Leidy, 1873); *M. elatus* Marsh, 1877; *M. hollandi* Peterson, 1913; *M. matthewi* Holland and Peterson, 1914; *M. merriami* Holland and Peterson, 1914; and additional presently undescribed species.

KNOWN DISTRIBUTION

Arikareean-Barstovian and possibly later faunas of North America (see Skinner, 1968, and Coombs, 1973, for later generically questionable material); Aquitanian-? of Eurasia.

DIAGNOSIS

1) Dental formula I 0/3, C 0/0, P 3/3, M 3/3; 2) molars intermediate in proportionate length and crown height between those of *Schizotherium* and *Ancylotherium*; 3) absence of a) crochet, b) labial rib on ectoloph between mesostyle and metastyle, and c) accessory cuspsules on M³ posterolingual to hypocone; 4) no hypoconulid on M₃; 5) frontals and parietals of skull without dorsal expansion; 6) Mc V present; 7) scaphoid never contacting Mc II, even during extreme carpal flexion; 8) volar process on lunate better developed than in *Ancylotherium*; 9) no dorsal flattening of metacarpals; 10) asymmetrical astragalus; 11) astragalus articulating distally only with the navicular; 12) metatarsals proportionately shorter than in *Schizotherium* and *Borissiakia*; 13) Mt III and Mt IV subequal in length; 14) Mt IV having ectocuneiform facet; and 15) proximal and medial phalanges of digit II of the manus fused to form a duplex in all except very young individuals.

DISCUSSION

Moropus differs from *Schizotherium* in characters 2, 4, 12, and 15; from *Borissiakia* in characters 3b, 3c, 11, 12, and 15; from *Phyllotillon* in characters 3a and 3b (but a crochet and posterior ectoloph rib are present only rarely in *Phyllotillon*); and from *Ancylotherium* in characters 1 (incisors only), 2, 3a, 3b, 6, 7, 8, 9, 13, and 14. *Moropus* also differs from *Borissiakia*, *Ancylotherium*, and *Schizotherium turgicum* in the retention of a trapezium in the manus in all species except *Moropus hollandi*; this bone was lost independently in several schizotheriine lineages. *Moropus*, like *Ancylotherium*, has a tendency to fuse the proximal and medial phalanges of digit II of the pes to form a smaller, more symmetrical duplex than that belonging to the manus. The species included in each of the Old World genera discussed above follows the treatment by Coombs (1974).

Two new schizotheriine genera have recently been named—*Huanghootherium* Tung et al. (1975) and *Gansuodon* Wu and Chen (1976). Both genera are based on upper molars and differ from *Moropus* in the following characters: larger size; greater crown height; smaller hypocone; more prominent, ridge-like cingulum lingual to the protocone. *Gansuodon* has a large crochet on M³, and *Huanghootherium* has a trace of one on M². All of the preceding differences from *Moropus* are shared similarities among *Gansuodon*, *Huanghootherium*, and *Ancylotherium*. *Ancylotherium pentelicum*, as figured by Thenius (1953), is almost as large as the type of *Gansuodon* and resembles it closely. The large M³ of *Gansuodon* compared to M² is probably not a valid difference from *Ancylotherium*, for M² and M³ of the type of *Gansuodon* may not be the same individual. *Huanghootherium* was distinguished especially by its tall ectoloph, whose height on M³ exceeds the width of the tooth. *Ancylotherium* also has very high-crowned molars, but possibly not so tall as in *Huanghootherium*; further comparison is necessary. Wide intraspecific ranges of variation are common in schizotheriines, and the Chinese material may in future best be viewed as species within *Ancylotherium*. It is not clear how *Gansuodon* and *Huanghootherium* might be related to probable *Ancylotherium* postcranials from China already figured by Bohlin (1936; an astragalus) and Colbert (1934, Figs. 13a, d, f; an Mt II and phalanges).

North American schizotheriines from the Arika-

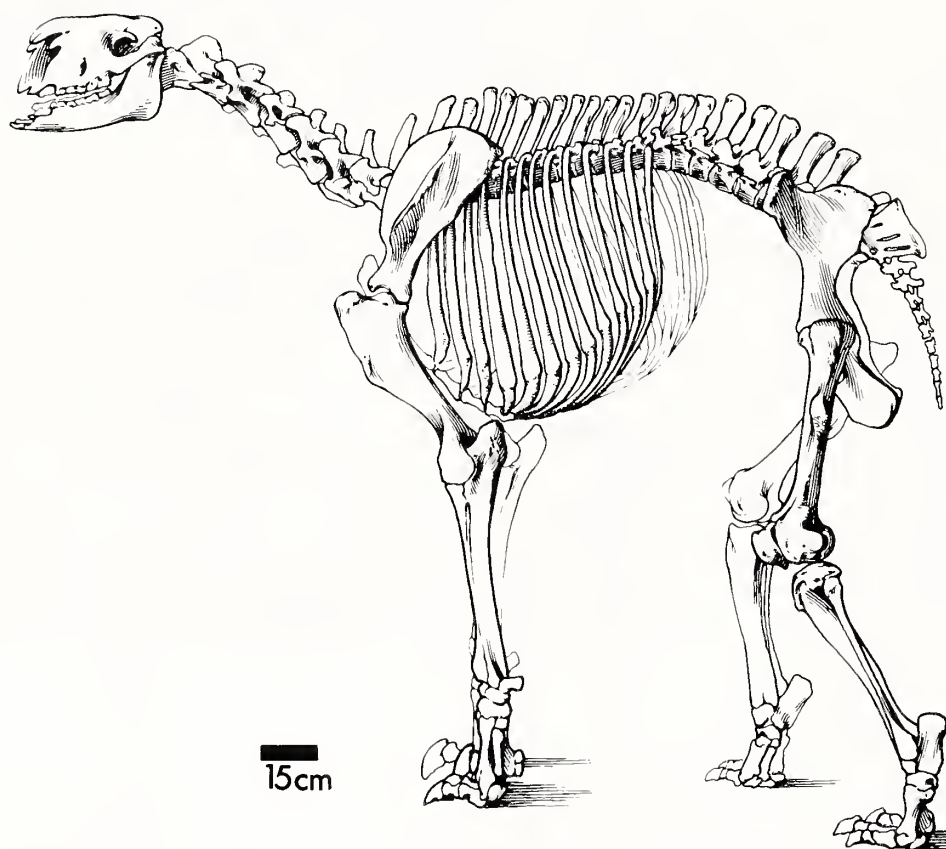


Fig. 2.—Mounted skeleton of *Moropus elatus*, AMNH 14,375, as reconstructed by Osborn (1919). Courtesy of the American Museum of Natural History.

recean onward form a distinct radiation, probably separate from Old World forms. A European Aquitanian representative of *Moropus* is also recognized (*Moropus* sp., Coombs, 1974). Both *Schizotherium* and *Borissiakia* are easily distinguished from *Moropus*, but there are problems in distinguishing Old World representatives of *Moropus* from *Phyllotillon* (known from limited material from the Burdigalian of Baluchistan and possibly later from Europe) and from *Ancylotherium* (*Metaschizotherium*).

Moropus elatus Marsh

- Moropus elatus* Marsh, 1877:250.
Moropus cooki Barbour, 1908:215.
Moropus petersoni Holland, 1908:810.
Moropus parvus Barbour, 1909:222.
Moropus elatus: Peterson, 1907b:733; Holland and Peterson, 1914:222.
Moropus petersoni: Holland and Peterson, 1914:226.
Moropus cooki: Osborn, 1917:131.

- Moropus cookei*: Osborn, 1919:251, Fig. 1.
Moropus cooki: Matthew, 1929:520; von Koenigswald, 1932:22.
Moropus elatus: von Koenigswald, 1932:22.
Moropus elatus, *M. petersoni*, *M. parvus*, *M. cooki*: Colbert, 1935:13; Belyaeva, 1954:49.
Moropus elatus: Coombs, 1974:275; Coombs, 1975:55.

LECTOTYPE

Mt II of YPM 13.081 (Fig. 18), collected by Hank Clifford in Nebraska, probably near the Niobrara River (see discussion of locality above), ?Harrison Formation, ?late Arikarean.

PARALECTOTYPES

YPM 24.631a–d, part of duplex of digit II manus, proximal phalanx, tuber of calcaneum, and proximal end of Mt III (Fig. 19). The paralectotypes were figured as part of the type by Holland and Peterson (1914:223–224).

HYPODIGM

YPM 24.632, cuneiform, patella, and distal end of Mc II (figured as part of the type collection by Holland and Peterson but not mentioned by Marsh, 1877); a large quantity of material, including complete skeletons, from the Agate Spring Quarries, Sioux County, Nebraska, in the Carnegie Museum of Natural History, American Museum of Natural History, University of Nebraska State Museum, and other museums; extensive dental and postcranial material (but no complete skeletons) from Morava Ranch Quarry, 18 mi east of Agate, Box Butte County, Nebraska, in the Frick Collection of the American Museum and the Pratt Museum, Amherst College; and additional fragmentary specimens from various localities in northern Sioux County, Nebraska. All referred specimens are from the Harrison Formation or Upper Harrison Formation (see above).

DIAGNOSIS

1) Chalicotheres at the middle to large end of *Moropus* size range; 2) upper molars more proportionately elongate than in *M. oregonensis*; 3) labial metaloph origin on unworn M^3 very near mesostyle; 4) no lingual cingula on lower molars; 5) trapezium present and well developed; 6) calcaneum with strong extension of narrow ectal facet onto tuber calcis; 7) navicular facet on tibial surface of cuboid without any proximal extension; 8) Mt II with ectocuneiform facet having primarily fibular orientation and an oblique tibial ridge present on the proximal part of the shaft; and 9) proximal and medial phalanges of digit II of the pes only occasionally fused (approximately 10% of cases).

DISCUSSION

Of the *Moropus* species discussed in this paper, *Moropus elatus* differs from *M. distans* in characters 1, 7, and probably 9, from *M. oregonensis* in characters 1 and 2, and from *M. hollandi* in character 5. Further, *M. elatus* has, on average, proportionately longer metatarsals than are known for *M. hollandi* (Table 6). Most of the other diagnostic features mentioned differentiate *M. elatus* from more advanced *Moropus* species like *M. merriami*.

Reasons for synonymizing *Moropus petersoni* Holland, 1908 (including its junior synonym *M. parvus* Barbour, 1909) with *M. elatus* were detailed by Coombs (1975). Individuals previously referred to *M. petersoni* are probably females of *M. elatus*.

Morphologic comparisons between the type of *M. elatus* and Agate material (below) provide evidence that *Moropus cooki* Barbour, 1908, is also a junior synonym of *M. elatus*.

I have not been able to locate the large scapula (CM 1776) described by Holland and Peterson (1914:230, 332, Fig. 77) as *Moropus* (?) *maximus*. This specimen, from the Agate Spring Quarries, is as figured different from all known scapulae of *Moropus*, despite the large amount of material and variation known. It is here thought to be either an aberrant specimen of *M. elatus* or does not belong to a chalicotherid. *M.* (?) *maximus* must be considered a *nomen dubium*.

Moropus elatus is the most completely known of all chalicotherid species. Agate material collected by the American Museum of Natural History after Holland and Peterson's (1914) monograph, as well as more recently collected specimens from other localities, provide additional information concerning intraspecific variation and other aspects of anatomy. For example, an *M. elatus* edentulous premaxilla, AMNH 11,321, verifies the ruminant-like vegetation cropping mechanism in this species (Coombs, 1978). Such new data are discussed in the present paper with a brief update of morphology already detailed by Holland and Peterson. This review will be especially useful for comparison with other *Moropus* species. No attempt at muscular reconstruction or detailed functional analysis is made here; these topics are reserved for a separate paper.

DESCRIPTION AND COMMENTS

Dentition

Interpreting specific taxonomic relationship and phylogeny on the basis of dentitions is very difficult within the genus *Moropus*. This difficulty is unfortunate, because in most cases teeth are better represented in the fossil record than limb elements. Teeth show a great amount of variation in morphology and relative proportions within a single population, in many cases combined with the lack of substantive changes in the teeth between populations, even over a long period of time. Yet changes in the limbs of the same animals have been much greater. It is often impossible to identify an isolated tooth or even several associated teeth below the generic level. All things considered, however, it does appear that a few regular changes in dentition occurred as North American chalicotheres evolved. Some of these changes are in pro-

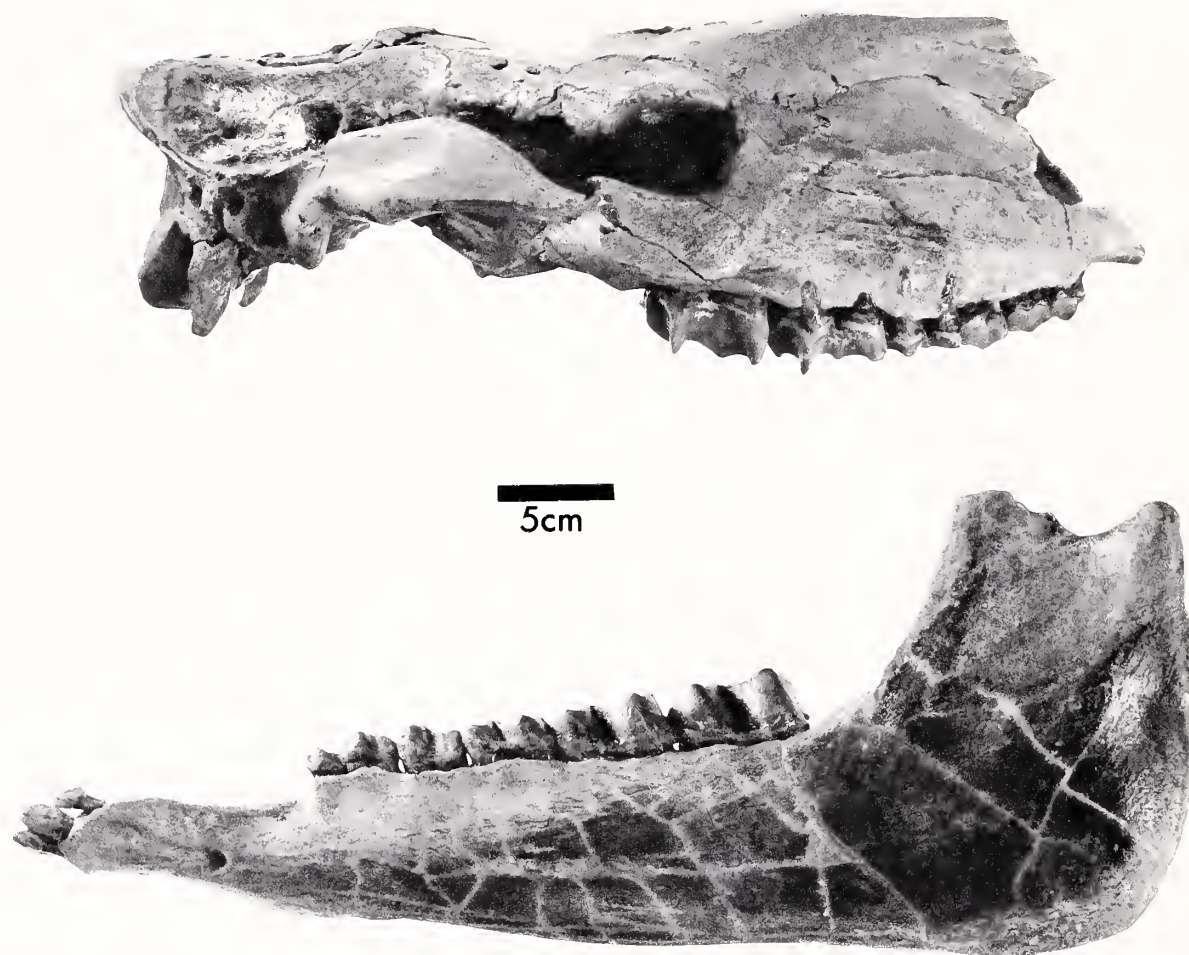


Fig. 3.—Top: right lateral view of skull of AMNH 11.322. Bottom: lateral view of left mandibular ramus of AMNH 14.427 (coronoid process broken). Both are *Moropus elatus* from the Agate Spring Quarries, Sioux Co., Nebraska.

portions, others in morphology, often in one part of the toothrow but not in another. Particularly important may be subtle changes in tooth wear (that is, which areas of a tooth are worn first and along what plane). At the same time, tooth wear is often a complicating factor because dentitions that would be similar at the same stage of wear may appear quite different at other stages of wear. For the most part treatment of North American chalicotheres dentitions has been inadequate, even when specimens were well known (see Holland and Peterson, 1914:245–250), but several European authors (Borissiak, 1946; Butler, 1965; and others) have given good accounts of variation among teeth of a single species. Possibly the lack of early treatment of dentitions of North American forms was a result of the problems created by intraspecific variation. The ter-

minology used in this section is diagrammed in Fig. 4; upper and lower teeth of *M. elatus* are shown in Fig. 3 and 5.

Upper Molars

*M*³.—This tooth is the least worn of the molars in any given toothrow and is easily recognized by the shape of its posterior part. It is approximately the same size as *M*², sometimes slightly longer or shorter; *M*² is in some cases relatively shortened because of wear. Both teeth are much larger than *M*¹ (see Table 1). In the progression from *M*¹ to *M*³ the anterior V of the W-shaped ectoloph becomes progressively longer compared to the posterior V. The change in proportions is particularly visible between *M*² and *M*³, for in the latter the ectoloph posterior to the mesostyle is not V-shaped but curves

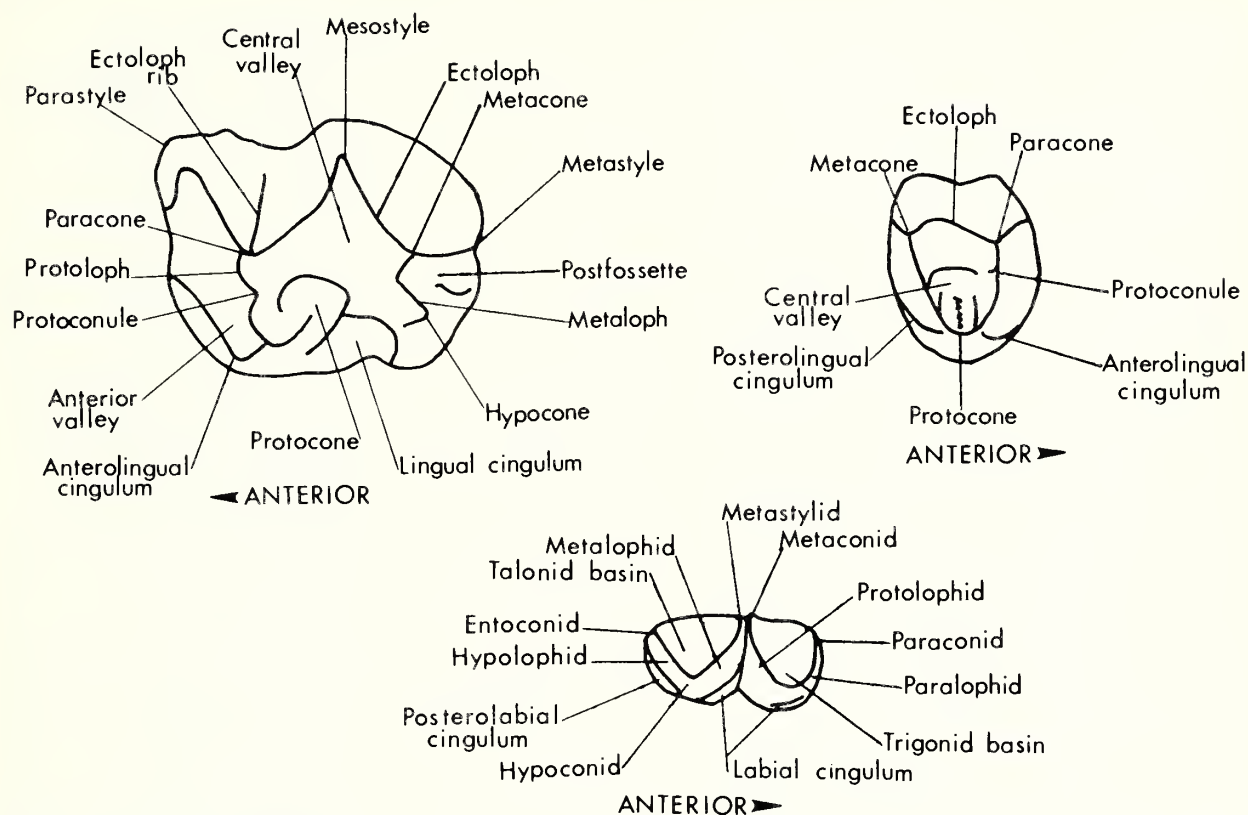


Fig. 4.—Diagrammatic upper molar, upper premolar, and lower molar of *Moropus elatus* giving dental terminology used in the text.

Table 1.—Lengths^a and widths^b (in mm) of upper cheek teeth of *Moropus elatus*, *M. hollandi*, and *M. oregonensis*.

Measurements	CM 2103(R) ^c	AM 9923(L) ^c	AMNH 11,322(R) ^c	AMNH 14,427(R) ^c	FMNH P12094(L) ^d	YPM 10,030a,b ^e	YPM 10,030 ^e
Labial length P ²	21.3	21.9	20.1	20.5	18.8		
Width P ²	21.0	20.6	20.3	16.2	16.0		
Labial length P ³	23.1	23.2	23.2	21.1	19.4	17.4	
Lingual length P ³	21.8	21.7	21.4	18.0	18.8	15.3	
Width P ³	28.3	29.1	26.9	26.0	24.4	20.3	
Labial length P ⁴	26.0	25.8	23.2	25.3	22.5	19.1	18.2
Lingual length P ⁴	24.0	24.2	22.3	22.2	20.3	16.5	17.7
Width P ⁴	32.6	32.1	29.9	29.8	26.6	23.1	23.5
Labial length M ¹	41.2	35.8	35.4	37.4	35.7	25.9	
Width M ¹	35.2	37.6	35.9	32.9	31.7	21.4	
Labial length M ²	55.9	45.7	53.0	55.3	49.6	36.5	
Width M ²	42.9	44.7	42.0	40.6	40.8	26.2	
Labial length M ³	59.8	54.0	51.6	54.4	48.3	36.5	
Width M ³	48.6	51.0	42.6	44.1	43.2	33.8	
Length premolar row	68.5	69.3	62.7	62.4	58.1		
Length molar row	144.3	131.5	128.3	136.2	130.1		
Length premolar row/length molar row	0.47	0.53	0.49	0.46	0.45		

^a Lengths are maximum anterior to posterior dimensions.

^b Widths are maximum labial to lingual dimensions, including mesostyle on molars.

^c *M. elatus* from the Agate Spring Quarries and Morava Ranch Quarry (AM 9923).

^d *M. hollandi* from near Jay Em, Wyoming.

^e *M. oregonensis*: YPM 10,030a = left P³-P⁴, right M³; YPM 10,030b = left M¹-M²; YPM 10,030 = holotype right P⁴.



Fig. 5.—Occlusal views of cheek teeth of *M. elatus*: A) left p_2 - M_3 of AMNH 14,427; B) left p_2 of AMNH 11,322; C) left p_2 of AMNH 9564; D) left p_2 - M_3 of AMNH 9922. A and D from Agate Spring Quarries, Sioux Co., Nebraska. B and C from Morava Ranch Quarry, Box Butte Co., Nebraska.

posterolingually. The ectoloph of M^3 is never worn posterior to the metacone. Correlated with the shortening of the posterior ectoloph, M^3 is transversely narrow in its posterior part. All of these features are common to other schizotheriine chalicotheres.

On M^3 both parastyle and mesostyle are very strongly developed, whereas the metastyle is comparatively weak. The paracone is usually taller than, and labial to, the metacone. On many specimens a weak labial rib passes from the base of the ectoloph to the tip of the paracone; there is in no case such a rib passing to the metacone. Development of the protoloph varies among specimens, and its structure is rapidly obscured by wear. In the least worn specimens a protoconule is developed on the protoloph just lingual to the paracone. In most unworn specimens the protoloph is continuous all the way to the protocone but somewhat depressed lingual to the protoconule. In others, slightly more worn, the protoloph is incomplete and there is no connection between protocone and protoconule. Where the protoloph is complete, it curves posterolingually from the protoconule to join the protocone's anterior margin. The protocone is a broad-based, conical cusp with a blunt-pointed tip, which lies barely in the anterior half of the tooth, posterior to the paracone and protoconule. The tip of the protocone is worn only after the lingual surface of the ectoloph is well worn and in the majority of specimens is untouched. Even where the protocone is not still connected to the protoloph, a weak ridge passes anteriorly from its tip.

The anatomy of the metaloph of M^3 is fairly uniform, the primary differences resulting from varying degrees of wear. No metaconule is developed in any of the specimens, and the hypocone forms the lingual end of the metaloph, its tip intimately connected to and about the same height as the crest. In a slightly worn specimen the labial origin of the metaloph from the ectoloph is close to the mesostyle (less than 10 mm). In an older individual, attrition has worn the mesostyle to increase the apparent angle of the fold and has moved the apparent metaloph origin posteriorly so that there is a greater distance between metaloph origin and mesostyle. In the most worn specimens, the original tip of the metacone has been worn off and the apparent metacone is positioned posterior to the original one. This change is because of the attrition of the ectoloph anterior to the metacone but not posterior to it; the ectoloph crest then passes directly posteriorly or

even posterolabially rather than posterolingually from the repositioned metacone.

Bordered by the lophs and cusps of M^3 are three valleys, two of which increase in size somewhat during wear. The largest of these is the central valley, lingual to the ectoloph between paracone and metacone, anterior to the metaloph and skirting the posterior base of the protocone. This furrow is open lingually between protocone and metaloph, where it forms a notch in the tooth's lingual outline; in worn specimens there may also be an anterior opening across the worn-down protoloph. Between the protoloph and anterior cingulum is a shallower valley. A third small valley, or postfossette, which decreases in size as wear progresses, is bordered by metaloph and ectoloph between hypocone and metastyle. No crochet, as described by Butler (1965:178) for *Chalicotherium rusingense*, is present in any specimen, although there is sometimes the hint of a very small crista.

Development of cingula varies, but in each specimen a very weak labial cingulum is present. The anterior cingulum is strong and forms a border for the anterior valley, curving posterolingually to skirt the protocone. Near the protocone it is variable. It may be notched anterior to the protocone to create an anterolingual exit for the central valley where the protoloph is worn down or very low; it may thicken and almost merge with the lingual wall of the protocone, sending off a branch to merge with the protoloph or with the small anterior ridge from the protocone tip; or it may retain its ridge-like cingulum character as it skirts the protocone lingually. In all cases it has some (though variable) ridge-like character along the posterolingual part of the protocone; it may then continue weakly to merge with the hypocone or disappear at the large lingual exit of the central valley [it is never so thickened as in *Ancylotherium* (*Ancylotherium*) *pentelicum*]. A posterior moderate to well-developed cingulum connects hypocone and metastyle and partially or completely closes off the posterior opening of the postfossette [similar to *Ancylotherium* (*Metaschizotherium*) *fraasi* but not as high as in *A. (A.) pentelicum*].

In those specimens where roots are visible there are three present—two small labial roots and a large anteroposteriorly elongated lingual one. The lingual root sends a connecting crest to the small posterolabial root.

M^2 and M^1 .—Both these teeth are similar morphologically to M^3 . In most specimens they are too

worn to give good evidence of structural details, but occasionally (CM 1707A, see Holland and Peterson, 1914:pl. 51) an unworn M^1 is preserved in association with a deciduous dentition. Where M^1 is unworn it appears larger than it does in a mature toothrow between P^4 and M^2 , where anterior and posterior margins of the tooth have been removed by wear. Prior to wear it is clear that a protoconule and complete protoloph are present, although these are quickly worn away, but the protoloph does not necessarily continue directly onto the protocone.

Heavier wear on M^1 and M^2 reduces the sharpness of the cusps and increases the relative size of the parastyle in comparison to that of M^3 . Because of wear on the ectoloph posterior to the metacone on these teeth, the size of the postfossette increases rather than decreases with tooth use. There is a slight notch on the metaloph between metacone and hypocone, and the hypocone is taller relative to the metaloph than on M^3 . Cingula vary in much the same way as on M^3 , and root development is also similar. On both M^1 and M^2 there is a labial ectoloph rib opposite the paracone but none opposite the metacone.

Upper Premolars

P^2 is worn very early in the life of the animal, and its unworn structure is therefore difficult to determine. Holland and Peterson (1914:245) described this tooth in fairly great detail, but their terminology is difficult to understand; the terms here follow those of Butler (1965:183) for *Chalicotherium rusinense* (see Fig. 5). In the least worn specimens (for example F:AM 54,449, AM 9,922—Fig. 5C) the ectoloph is nearly straight (not W-shaped). The paracone is in line with the metacone, and there is a very low parastyle. Lingual to the paracone and connected to it by a short crest is a cuspule, probably the protoconule, which is not visible in more worn specimens, though traces of it remain. The single lingual cusp, or protocone, is close to the posterior border of the tooth. Because of its location and because it is connected by a strong crest (metaloph?) to the ectoloph posterior to the paracone, it looks more like a hypocone than a protocone. Labially the cingulum is very weak, but between the parastyle and protocone a prominent cingulum is present on the anterior and lingual edges of the tooth. A small posterior cingulum closes posteriorly the valley between protocone and metacone. The most obvious variation among P^2 specimens of this species is the occasional in-

creased development of the protoloph lingual to the protoconule and consequent broadening of the anterior part of the tooth (particularly well shown by CM 2103, the Agate Quarry specimen figured by Holland and Peterson, 1914:pl. 49). In this specimen the protoloph is in some places as tall as the protocone but is separated from the protocone by a deep, broad valley. At its lower, lingual end the protoloph merges with the cingulum, which skirts the protocone lingually.

P^3 and P^4 are very similar to one another, but P^4 is larger and less worn. Its ectoloph has a rudimentary W-shape, formed by differences in height of the various points rather than by changes in curvature or slant of the labial wall, which is still quite straight and flat. The paracone is slightly taller than the metacone, and a medium-sized parastyle is developed. Most of the early wear on the tooth is on the lingual side of the ectoloph but does not obscure relations with the lingual side of the tooth. The protocone, the only lingual cusp, is large and crescent-shaped and is the last part of the tooth to be worn. It is connected to the ectoloph by two crests, of which the protoloph is taller in some specimens, the metaloph in others. Both lophs are curved and merge into ectoloph and protocone at either end. Enclosed by ectoloph, protoloph, metaloph, and protocone is a deep central valley. Forster-Cooper (1920) noted a weaker metaloph than protoloph on P^3 and P^4 of *Phyllotillon* and used this character to differentiate *Phyllotillon* from *Chalicotherium*. Variation of this character within *Moropus elatus* suggests that such a distinction between *Phyllotillon* and *Moropus* does not apply.

As in P^2 , the cingulum is the most variable feature of P^4 , although in all specimens the labial cingulum is extremely weak. In CM 2103 the lingual cingulum is very strong and the tooth is therefore anteroposteriorly expanded in its lingual part. The anterolingual cingulum is here taller than the posterolingual one. Lingual to the protocone the cingulum loses its ridge-like nature at two points where it nearly merges with the lingual wall of the protocone. Between these points it is separated from the protocone by a small pit. In other specimens (for example, AMNH 11,322, Fig. 5) the cingula are in general much weaker, and in others the posterior cingulum is more strongly developed than the anterior. The lingual cingulum may also remain completely distinct from the protocone.

The smaller P^3 has a less W-shaped ectoloph, a weaker parastyle, and a consistently weaker ante-

rior than posterior cingulum. Variations among specimens of P^3 seem generally linked in the same individual to those of P^2 and P^4 .

Lower Molars

Lower teeth were given less attention by Holland and Peterson (1914) than upper teeth, but at the same time these teeth provide fewer features of taxonomic value. M_3 , the least worn lower molar, is approximately the same size as (slightly larger than) M_2 ; both are larger than M_1 . The trigonid is shorter but not narrower than the talonid; each consists of a V-shaped crescent of straight to slightly curved lophids. Trigonid and talonid join at the metaconid-metastylid. The metaconid, the tallest point on the trigonid, is sloped gradually anteriorly so that its base partly closes the lingual opening of the trigonid basin. In an unworn specimen, the protoconid, slightly anterior to the metaconid, is nearly as tall as the metaconid, but in a worn specimen it is considerably lower. The lowest cuspid of the tooth, the paraconid, does not rise above the level of the paralophid; usually the paralophid is the most curved of the four lophids.

On the talonid, the highest point is the metastylid, which in unworn specimens is completely separated from the metaconid at its tip. In more worn teeth the two cuspids are more continuous but still can be distinguished by the grooves between them on both labial and lingual sides. Of approximately equal height but lower than the metastylid are the hypoconid and entoconid, the former slightly anterior to the latter but both well posterior to the metastylid.

The labial part of M_3 is more rapidly worn down than the lingual part. Protoconid and hypoconid are worn by the ectoloph of the corresponding upper tooth near parastyle and mesostyle respectively and are eventually abraded to below the level of the lingual cuspids, even the paraconid. Trigonid and talonid basins gradually disappear. As wear progresses the lingual cuspids also become more worn, particularly the metaconid and metastylid, which cut across the lingual end of the protoloph of the upper molar. Finally the entire crown is worn flat.

Cingula on M_3 and the other lower molars vary among individuals. They are in all specimens strongest posteriorly, anterolabially, and on the labial side between the bases of protoconid and hypoconid. In many of the specimens no further cingula are visible, but in some the cingulum forms a well-defined ridge all around the labial base of the

tooth. In general, the Morava Ranch Quarry specimens seem to have slightly greater cingulum development than those from the Agate Quarries. On all specimens there is practically no development of a lingual cingulum except at the base of the paraconid, where a weak one may be visible.

Where known in an unworn condition, M_1 and M_2 are very similar to M_3 , but metaconid and metastylid are less deeply separated.

Lower Premolars

P_4 is very similar to the molars but differs in several ways. Most importantly, the talonid is reduced in length and height so that it is about the same length as the trigonid; its posterior part is particularly shortened so that the entoconid lies directly lingual to the hypoconid. Both of these cuspids are lower compared to metaconid-metastylid than are their counterparts on the molar teeth. Metaconid and metastylid are barely distinct at their tips and rapidly become confluent during wear. On the trigonid the paraconid is so low or so rapidly worn away that it is not visible. On the labial surface of the tooth the groove between trigonid and talonid slants strongly posteriorly toward its base, thus showing an increase in slant over that in M_1 , which in turn has more slant than on M_2 or M_3 . There is a strong ridge-like cingulum all along the labial base of the talonid, ascending at its anterior end opposite the base of the protoconid.

P_3 continues the trend away from molar morphology begun by P_4 . Here the talonid is shorter than the trigonid as well as lower in height, but it exceeds the trigonid in transverse width. The talonid has only a very small basin which is lost very early during wear to form an oblique flat wear surface. Both posterior cuspids, particularly the entoconid, are very low and are transversely aligned. The trigonid, in contrast to that of P_4 , has a well-developed paraconid that is approximately as tall as the protoconid and is not rapidly worn away. No separate metastylid is developed. The groove between trigonid and talonid is oblique but shallow, and there is a well-defined cingulum along the labial base of the talonid.

On P_2 only the protoconid forms a well-developed cuspid, and the talonid is rudimentary. Neither trigonid nor talonid basin remains, for all cuspids are in a straight antero-posterior line. Anterior to the protoconid, at the anterior edge of the tooth, is a distinct but small paraconid. Posterior to the protoconid, at the end of a crest, is the low, indistinct



Fig. 6.—(A and B) Ventral views (anterior at top) of atlases of A) *M. elatus*, AMNH 14,378, and B) *M. hollandi*, FMNH P13000. (C and D) Occlusal views of deciduous teeth of *M. elatus*: C) right dp_2 - dp_4 of AMNH 86,099 and D) right dp^2 - dp^4 of AMNH 94,232. A, C, and D from Agate Spring Quarries, Sioux Co., Nebraska; B from vicinity of Jay Em, Goshen Co., Wyoming.

hypoconid. On this tooth there is a weak lingual cingulum opposite trigonid and talonid, and on this cingulum there may be occasional traces of a metaconid and/or entoconid. Compared to the trigonid, the talonid is very short. As Holland and Peterson (1914:243) mentioned, the border of the mandible descends sharply anterior to P_2 , and there is a long diastema between this tooth and the lower incisors.

Incisors

Of the anterior teeth, only the three lower incisors are present. Their morphology has been discussed in association with an edentulous premaxilla, AMNH 11,321, from the Agate Quarries (Coombs, 1978). *Moropus elatus* had a cropping mechanism very similar to that of modern cervids and bovids, except that no lower canine was present. There is some evidence (AMNH 11,322) that in aberrant cases a procumbent lower canine or deciduous incisors might have been retained in line with the incisor row.

Deciduous Teeth

Upper teeth of *M. elatus* juveniles are known from at least five specimens (CM 1707A, CM 1743, CM 1747, CM 1738, AMNH 94,232). Both dp^3 and dp^4 strongly resemble the permanent molars but are smaller and more symmetrical and quadrate than M^1 ; the size difference between dp^4 and M^1 is greater than that between dp^3 and dp^4 . Because of wear on dp^3 , the protoconule is not visible and the protoloph is incomplete in all known specimens. On dp^4 there is, in the least worn specimens, a visible protoconule and a very low (already almost worn away) continuation of the protoloph to the protocone. A tiny anterolingual cuspule is present on the protocone of dp^4 in some cases (CM 1743). Wear on the metaloph causes the hypocone to be taller than the rest of the loph. On all specimens of dp^3 and dp^4 , the labial cingulum is absent.

The elongated, subtriangular dp^2 resembles the permanent P^2 more than it does the other deciduous teeth. As in P^2 , dp^2 is broadest in its posterior part, due here to strong development of the hypocone, an isolated conical cusp; any metaloph has been rapidly worn away by wear cutting down the lingual face of the ectoloph. The ectoloph has the parastyle in a straight line with the barely distinguishable paracone and metacone; strong development of the parastyle causes the anteroposterior elongation of the tooth. There is a small protocone anterolingual to the paracone and connected to it by a short crest.

Table 2.—Maximum anterior-posterior lengths (in mm) of lower deciduous teeth (plus M_1 and M_2 where preserved on these jaws) of *Moropus elatus* and *Moropus* sp. (from St. Gérard Le Puy, France; Coombs, 1974).

Measurements	CM 1755	CM 1759	AMNH 86,098	AMNH 86,099	<i>Moropus</i> sp.
Length dp_2	—	14.4	—	14.3	14.0
Length dp_3	26.4	28.2	27.2	27.6	broken
Length dp_4	29.2	29.2	29.4	—	20.5
Length dp_2 - dp_4	67.4	70.8	—	69.5 ^a	54.2
Length M_1	35.3	35.1	—	—	—
Length M_2	—	46.7	—	—	—

^a Approximate value.

Posterior and lingual cingula are strong, but there is no anterior cingulum.

A relatively large number of mandibles with deciduous teeth are available for this species. dp_4 , though considerably smaller than M_1 , is strongly molariform. Its metaconid and metastylid are clearly separate at the tips, and in unworn specimens a small paraconid tip is visible; this anterior cuspid is rapidly worn away, however, as the trigonid of dp_4 is compressed against the talonid of dp_3 . Both trigonid and talonid basins are well defined, the latter slightly larger and deeper than the former. dp_3 , although more molariform than its permanent counterpart, differs in several respects from dp_4 , particularly in the trigonid. Although the tooth retains the double crescent shape of the molars and both trigonid and talonid basins are present, the former is very shallow. Compared to the talonid, the trigonid is very narrow, and its paralophid is elongated so that the paraconid lies well anterior to the protoconid. On dp_3 the paraconid is almost as strongly developed as the protoconid and is not worn down rapidly. Thus the talonid of dp_3 is similar to that of dp_4 and the permanent molars, while the trigonid more closely resembles the permanent P_3 . Metaconid and metastylid are separated at their extreme tips, and the cingula are like those of molars. The small dp_2 is in most specimens strongly worn (AMNH 86,099 retains it in good condition, see Fig. 6). It is not at all molariform and strongly resembles the permanent P_2 . Paraconid, protoconid (the tallest cuspid), and hypoconid are in a straight anteroposterior line. A well-defined crest joins the paraconid and protoconid. Although neither metaconid nor entoconid is visible, there is a trace of a talonid basin on dp_2 that is not present on P_2 .

Skulls (see Fig. 3)

Holland and Peterson (1914) gave some details of the cranium of CM 2103, a well-preserved (although dorsoventrally crushed) specimen of a large individual from the Agate Quarries. Some of the subsequently recovered material in the American Museum of Natural History shows remarkable preservation of the basicranium, and an *M. elatus* skull (AM 9923) has also recently been excavated from Morava Ranch Quarry. Comparison of all these skulls with later North American specimens should be profitable when all the material is fully prepared. There are a number of similarities among *M. elatus* skulls to those of *Chalicotherium* (Filhol, 1891; Colbert 1934) and *Borissiakia* (Borissiak, 1946), which illustrates the basic unity of cranial structure among all chalicotheriids. Among general chalicothere features are the arrangement of basicranial foramina, the extension of the flat glenoid fossa onto the ventral surface of the zygomatic arch, the partial but not complete posterior closure of the orbit, and the presence of a long medial ventral crest from the internal nares through the prephenoid.

The lateral view of the skull of AMNH 14,375 figured by Coombs (1978) shows uncrushed skull proportions of *M. elatus* and reconstructs the edentulous premaxilla in position. The gently curved dorsal surface of the skull of *M. elatus* lacks any suggestion of doming or elaboration. The stylomastoid foramen, anterior to the base of the paroccipital process and posterior to the enclosed auditory tube, was not mentioned by Holland and Peterson. The condylar foramen of Holland and Peterson is more usually termed the hypoglossal foramen (see Sisson and Grossman, 1953:72). In all cases the bullae are large and rounded, but the paroccipital processes, although well developed, are variable. In some cases (CM 2103) they are concave anteriorly and convex posteriorly, but in other specimens the exact reverse is true. Of particular note in *M. elatus* is the consistent position of the internal nares and the infraorbital foramina in all specimens examined. In adult individuals the palatines extend posterior to M^3 , and the internal nares are therefore posterior to M^3 also, at least no farther forward than the hypcone of M^3 . Infraorbital foramina lie on the snout opposite the anterior part of M^2 .

Mandibles

Holland and Peterson compared lower jaws of *M. elatus* to those of *Equus* and *Ancylotherium*. With

a few minor differences, mandibles of *M. elatus* are very similar to those of other *Moropus* species. Basic features of the mandible are 1) a narrow anterior part with a short symphysis ending opposite or anterior to P_2 , 2) a long (about as long as and often longer than the premolar row), curved diastema between I_3 and P_2 with the mental foramen (sometimes two) lying slightly posterior to its midpoint, 3) base of P_2 raised somewhat above the level of the diastema, 4) labial and lingual sides of jaw primarily flat but slightly convex below cheek teeth, 5) base of ascending ramus broad, rugose, 6) coronoid process curved posteriorly with long anteroposterior extent, 7) articular condyle flat dorsally with dorsal and posterior parts meeting at almost a right angle, 8) temporal fossa somewhat and pterygoid fossa more strongly excavated, 9) dental foramen large, and 10) angle narrow, flat, not projecting notably below the remainder of the jaw margin.

Vertebrae and Ribs

Vertebrae and ribs of *M. elatus* were described in great detail by Holland and Peterson (1914) and will not be described here. Trends in *Moropus* cervical vertebrae from II-VII include a very gradual shortening of the centrum, elongation, narrowing, and increased anterior slant of the neural spine, a decrease in the ventral keel, and a slight increase in width but simplification of the transverse process. Between cervical VI and VII the vertebralarterial canal is lost. General chalicothere characters of the cervical vertebrae are elongated centra, oblique anterior and posterior facets on the centra, and a strongly developed ventral keel on anterior vertebrae.

Twenty-one dorsal vertebrae are present in *M. elatus*. Of these, 15 bear ribs (XV has an anterior but no posterior caput facet): I-XV represent thoracics and XVI-XXI lumbar. Some trends represented along the course of the dorsal vertebrae are the following: 1) the neural spine increases in length from I-III, decreases from IV-XIII, then increases again into the lumbar series from XIII-XIX and decreases again from XIX on; 2) the neural spine slants progressively more posteriorly from VI-XIII, but then decreases its angle from the vertical to stand almost erect at the last thoracic (XV), and then is nearly straight or very slightly anterior or posterior slanted through the lumbar series; 3) the ventral keel decreases along the most anterior dorsals; 4) there is an increase in the transverse process and separation of a metapophysis from dorsal V

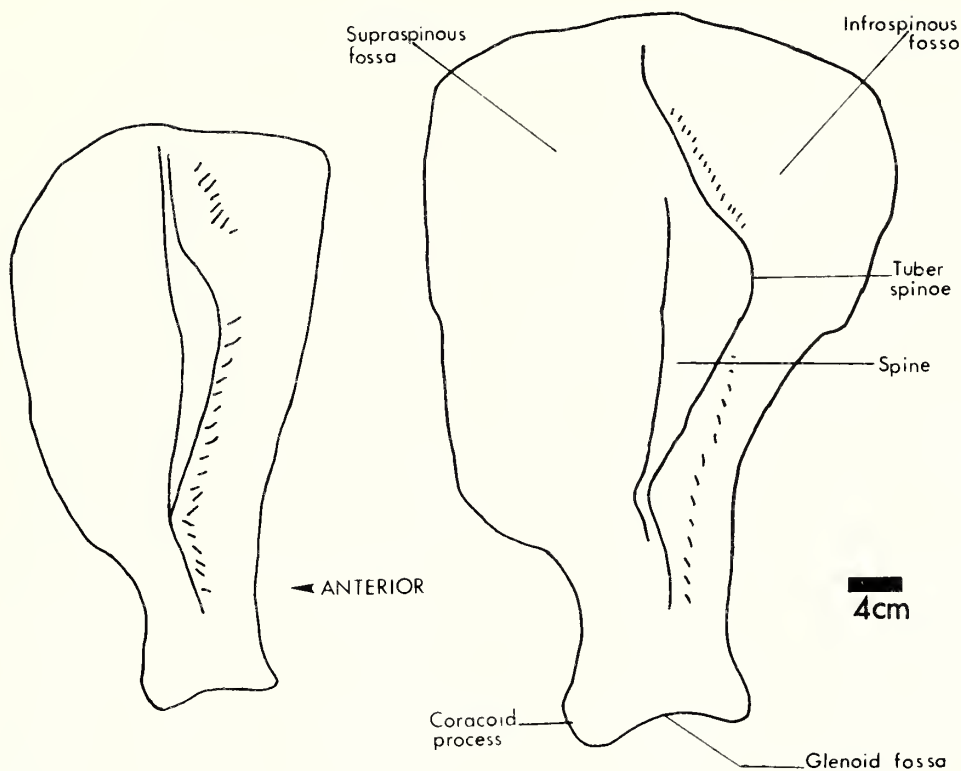


Fig. 7.—Lateral views at scaled size of *M. elatus* scapulae of a small individual (?female), CM 1700, on left, and a large individual (?male), CM 1604, on right. Modified from Holland and Peterson (1914, Fig. 76 and pl. 65).

onward; 5) from VI–XV the exit notch for the spinal nerve forms a progressively larger bony circle; 6) the neural spine becomes less laterally compressed from IV–XII but more compressed from XII onward; 7) the prezygapophyses migrate onto well-developed metapophyses from XVI onward, whereas the postzygapophyses of these vertebrae are directed more laterally; 8) the centrum becomes less triangular and more oval and dorsoventrally compressed from XIX–XXI.

Well-preserved sacra show fusion of five vertebrae; the transverse processes of the anterior four are enlarged and strongly fused together to form a strong attachment to the ilium. The first sacral is especially broad. The neural spines, which are tightly fused together, become progressively more posteriorly slanted, whereas the size of the centrum decreases as you follow the sacral series posteriorly. The metapophyses on sacral I bear an articular surface for the posteriormost lumbar, but posterior to sacral I they decrease in size and disappear.

No caudal vertebrae are known for any *Moropus* species outside *M. elatus*, but several belonging to

M. elatus are preserved, some fused to the sacrum. Known specimens all suggest a small, short tail.

Forelimb

Scapula.—All *M. elatus* scapulae are quite similar in general structure. Care must be taken in assessing morphological differences, for here in particular many structural variations are the result of differential allometric growth in animals of different absolute size, either different sexes or growth stages. An example of the differences between scapulae of the same species is shown in Fig. 7, individuals referred by Holland and Peterson to different species. In the larger specimen the tuber spinae is heavier and more posteriorly curved and the upper posterior border of the infraspinous fossa is more rounded, thick, and rugose—adaptations to greater weight bearing (see Osborn, 1929:740–741) in the larger heavier animal.

Scapulae have the following general features: 1) a circular to oval glenoid fossa with a moderately developed coracoid process just anterior to it; 2) an indented anterior border below the spine; 3) ante-

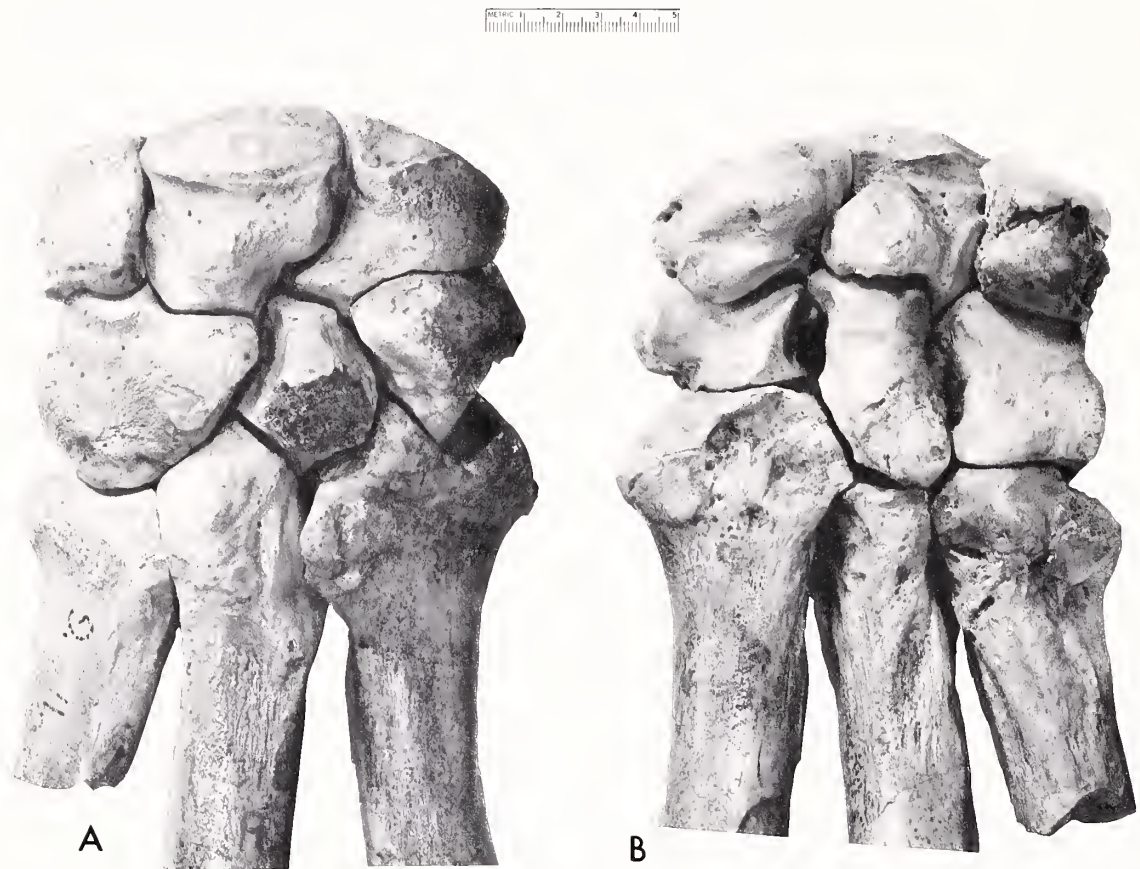


Fig. 8.—Dorsal (A) and volar (B) views (excluding trapezium, pisiform) of right carpus of AMNH 14,378, *M. elatus*, from the Agate Spring Quarries, Sioux Co., Nebraska. Labels in Fig. 9.

rior border of blade slightly more convexly rounded than posterior border; 4) upper (proximal) end slightly squared to gently rounded; 5) well-developed spine with posteriorly reflected tuber spinae; 6) supraspinous and infraspinous fossae of subequal size; 7) subscapular surface gently concave with a slightly convex ridge in the anterior or middle part. *M. elatus* has a more strongly posteriorly reflected tuber spinae than is known in other *Moropus* species.

Humerus (Fig. 13A).—The humerus of *Moropus*, unlike the femur, is not easily confused with humeri of contemporary perissodactyls (for example, of rhinoceroses). Compared to the probable weight of the animal and the size of the proximal articulation and greater tuberosity, the shaft is very long. Even more unusual is the comparatively strong development of the entepicondyle, otherwise reduced or absent in all but the most primitive ungulates. The distal trochlea is transversely very broad and is not

deeply grooved; the anterior part of the trochlea (capitulum), with which the radius articulates, is particularly wide. Holland and Peterson (1914:334–335) mentioned the following important features of the humerus of *M. elatus*: large, rounded head; well, but not unusually, developed greater tuberosity; relatively shallow but broad bicipital groove; prominent deltoid ridge extending well down the shaft and flexed posteriorly; prominent ectocondylar ridge (but not as strong as in most other perissodactyls); deep olecranon fossa; shallow coronoid fossa; plus the very important characters of the distal end mentioned above.

Radius-ulna.—Although a number of radii and ulnae are available, there are few consistent differences from other *Moropus* specimens, which can be regarded as of taxonomic value. In many cases only a single radius or ulna (often broken) is known; in other cases the two bones are solidly fused, usually at the distal end and sometimes also for part of

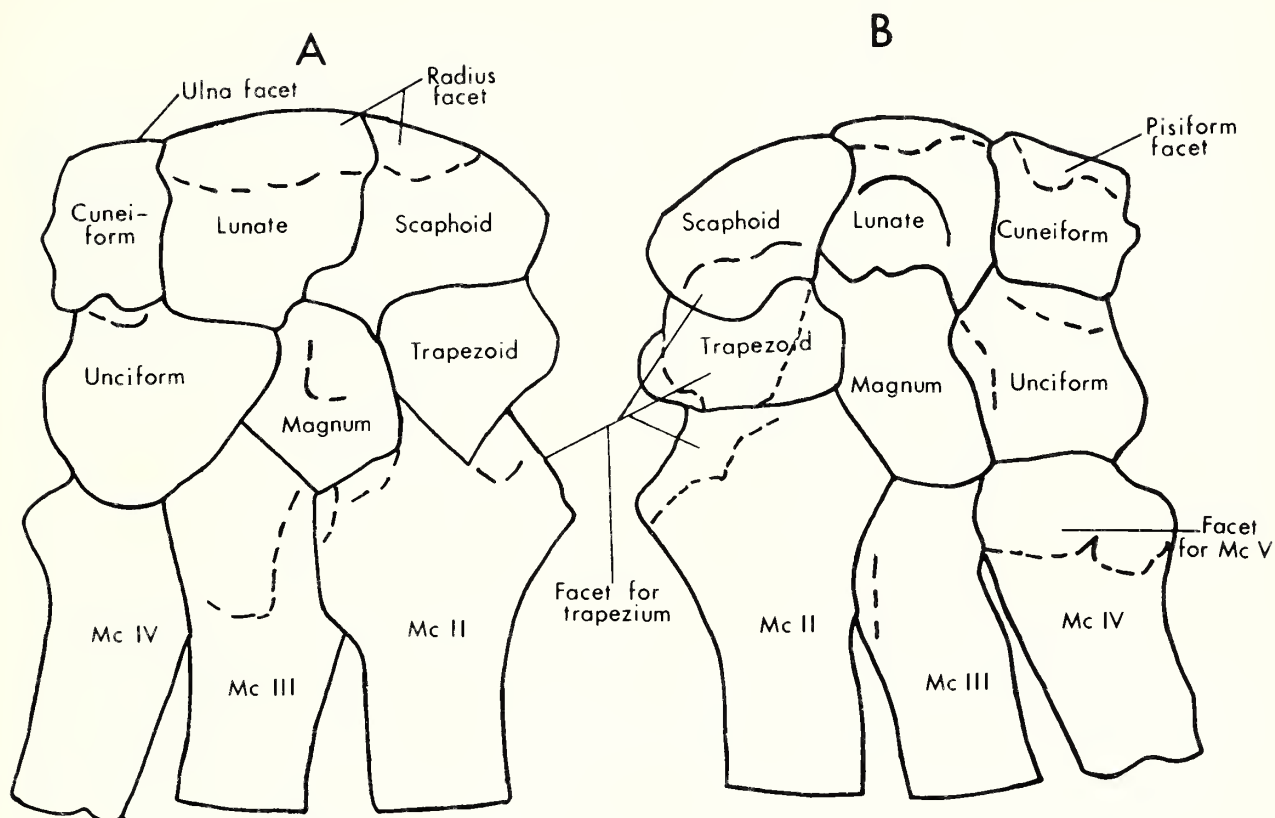


Fig. 9.—Labeled drawing of dorsal and volar views of right carpus of AMNH 14,378 shown in Fig. 8.

the shaft. There does not seem to be any quarry or locality correlation between groups in which more or less fusion occurs; rather, fusion may be correlated with the age of the animal. Whether or not strong fusion occurred does not seem to be functionally critical, for in any case the facets between the two bones at their proximal ends would allow little or no movement between them, certainly no rotation of the radius.

General features of the ulna include rather short but heavy olecranon process, prominent anconeal process, deep semilunar notch with strong expansion near the radius facet, radius facet distal and at an acute angle to semilunar notch and forming a deep articular fossa, shaft subtriangular in section, distal end narrow with cuneiform facet flat and adjacent (across a 90-degree arc) to the pisiform facet on the posterior (volar) surface. Some radius features include proximal and distal ends broader than shaft articular surface for humerus with broad, slightly concave ulnar (lateral) part and narrower, flatter radial (medial) part, coronoid process weak, facet for ulna with proximally oriented central

tongue and posteriorly (volar) oriented radial and ulnar parts (somewhat variable), distal end with dorsal groove between scaphoid and lunate facets, lunate facet more concave and of greater dorsovolar extent than scaphoid facet.

Carpals.—Carpal elements of *M. elatus* were described and figured by Holland and Peterson (1914:337–339), but additional material has given a more accurate view of the absence of significant variation among specimens and the general usefulness of manus and pes elements in taxonomy. Therefore the most salient features of the carpals are worth rediscussing here as a basis for taxonomic and functional work to follow (see Figs. 8–12).

On the scaphoid the weakly convex articular surface for the radius covers all of the proximal surface except for a rugose protuberance at the ulnovolar angle (Fig. 10A). The radiovolar surface bears a small but well-defined, distally slanting, convex facet for the trapezium (Fig. 8B). Adjacent and distal to the trapezium facet is the saddle-shaped trapezoid facet, a large facet, which reaches distally onto the radial side of the distal process (Fig. 10B, pal-

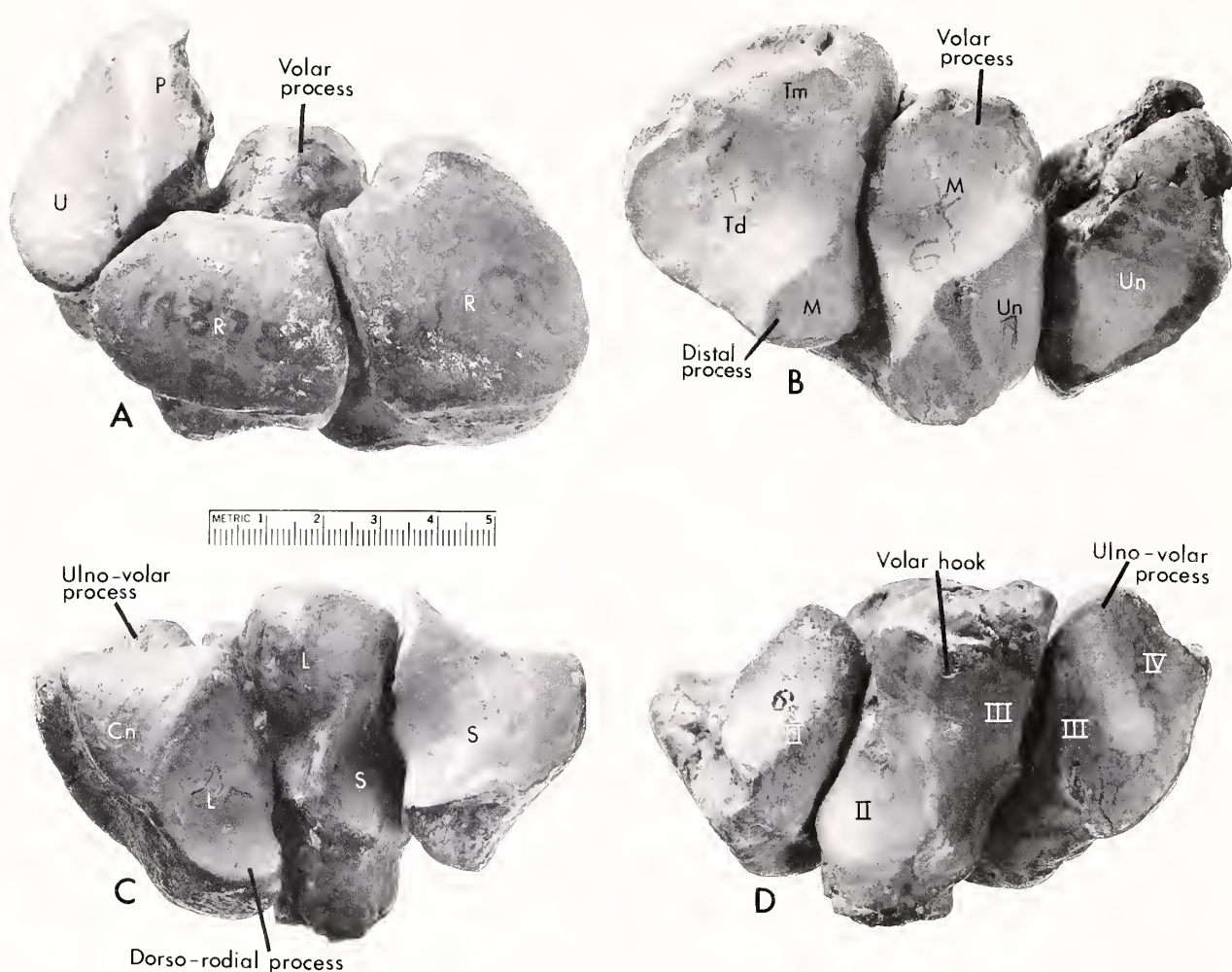


Fig. 10.—Proximal (A and C with radial edge at right) and distal (B and D with radial edge at left) views of right cuneiform, lunate, scaphoid (A, B) and right unciform, magnum, trapezoid (C, D) of *M. elatus*, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska. Abbreviations for facets in Figs. 10–12, 22, and 24–26 are as follows: R, radius; U, ulna; P, pisiform; S, scaphoid; L, lunate; Cn, cuneiform; Un, unciform; M, magnum; Td, trapezoid; Tm, trapezium; II, Mc II; III, Mc III; IV, Mc IV; V, Mc V.

mar process of Holland and Peterson). Of the two facets for the lunate on the ulnar surface (Fig. 11A), the proximal oval one stands on a low platform and is particularly prominent at its volar edge. The more distal lunate facet occupies the ulnar surface of the distal process and curves from the magnum facet in a proximoulnar direction so that in its most proximal part it borders the volar edge of the trapezoid facet. Between proximal and distal lunate facets, the ulnar surface of the trapezoid is depressed. Because the large distal process is squared, the facet for the magnum on its distal end is flat to slightly convex, bordered on one side by the trapezoid facet and on the other by the distal lunate facet.

On the lunate, the proximal articulation, which is for the radius, is of suboval shape and convex in

all directions, especially strongly so in the dorsal to volar direction (Fig. 10A). Very prominent in a proximal view is the volar process near the distal edge, which has a facet (for the magnum) on its distal but not on its proximal surface (Fig. 10B). Of the two scaphoid facets on the radial surface (Fig. 11B), the proximal one is large and adjoins the radius facet across a prominent keel; separated by a groove from the proximal facet, the distal scaphoid facet varies slightly in position in different specimens, sometimes passing along the radiodistal surface of much of the volar process but barely distinguishable from the magnum facet except on the volar process. On the most distal part of the radial surface of the lunate, the magnum facet curves onto the distal surface of the volar process, where it

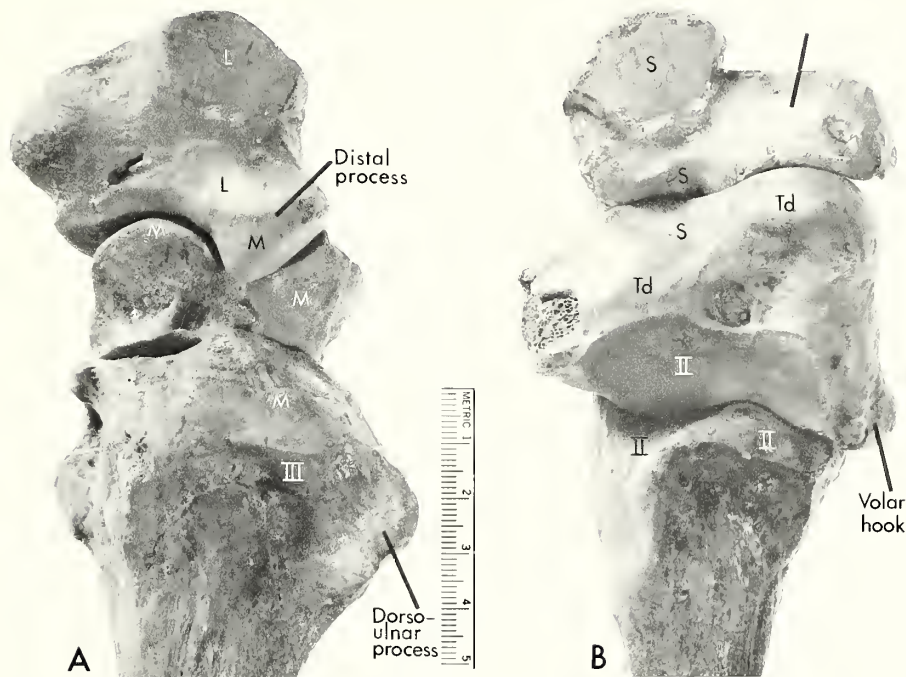


Fig. 11.—A) Ulnar view of right scaphoid, trapezoid, and Mc II (dorsal edge at right), and B) radial view of right lunate, magnum, and Mc III (dorsal edge at left) of *M. elatus*, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska. See Fig. 10 for facet abbreviations. Unlabeled line points to volar process of lunate.

forms a concave, cup-shaped facet separated by a ridge from the distal lunate facet (Fig. 10B). All along its most distal and ulnar edges the magnum facet is divided by a beak-like ridge from the unciform facet (Figs. 10B, 12A). The unciform facet has two parts, the dorsal part flat to convex and with an almost entirely distal orientation, the volar adjoining part slightly concave and curving onto the ulnar side of the bone, where it is weakly distinguishable from the cuneiform facet. Flat to weakly convex and on a low platform, the cuneiform facet forms a D-shaped tongue onto the ulnar surface of the lunate (Fig. 12A).

Several cuneiforms from the Agate Quarries and Morava Ranch Quarry were compared with YPM 24,632, which is part of the type collection of *M. elatus* and closely resembles the more recently collected specimens. This bone is very deep in the dorsal to volar direction but is transversely narrow. At the dorsoradial angle and volar edge the cuneiform tapers to a blunt point, giving the bone a wedge-shaped appearance in proximal view (Fig. 10A). The dorsal and ulnar surfaces of the bone are rough, but not strongly rugose, and on the distal part of the ulnar surface is a blunt roughened protuberance

for the attachment of muscles or ligaments (Figs. 8A, 10B). There is another, smaller protuberance near the proximal edge of the narrow volar surface. Both pisiform and ulna articulate with the proximal surface of the cuneiform (Fig. 10A). The relative amounts of the proximal surface occupied by each varies in the specimens examined, but in each case the more dorsal facet, for the ulna, is larger. A very weak diagonal ridge separates the two facets, and the pisiform facet is raised slightly above the ulna facet. Both facets are wedge-shaped, the slightly concave ulna facet narrowest in the volar direction, the weakly convex pisiform facet narrowest dorsally. On the distal surface of the cuneiform (Fig. 10B), the unciform facet is concave in the dorsal to volar direction and closer to the dorsal than to the volar edge of the bone. There is only one, tongue-like facet for the lunate, at the distal edge of the radial surface (Fig. 12B), and adjoining the unciform facet at a right angle. No second, more proximal lunate facet is observable.

On pisiform specimens of *M. elatus*, the cuneiform facet is parallel to the long axis of the pisiform and the adjacent ulna facet perpendicular to it. Both surfaces curve in tongues away from their straight

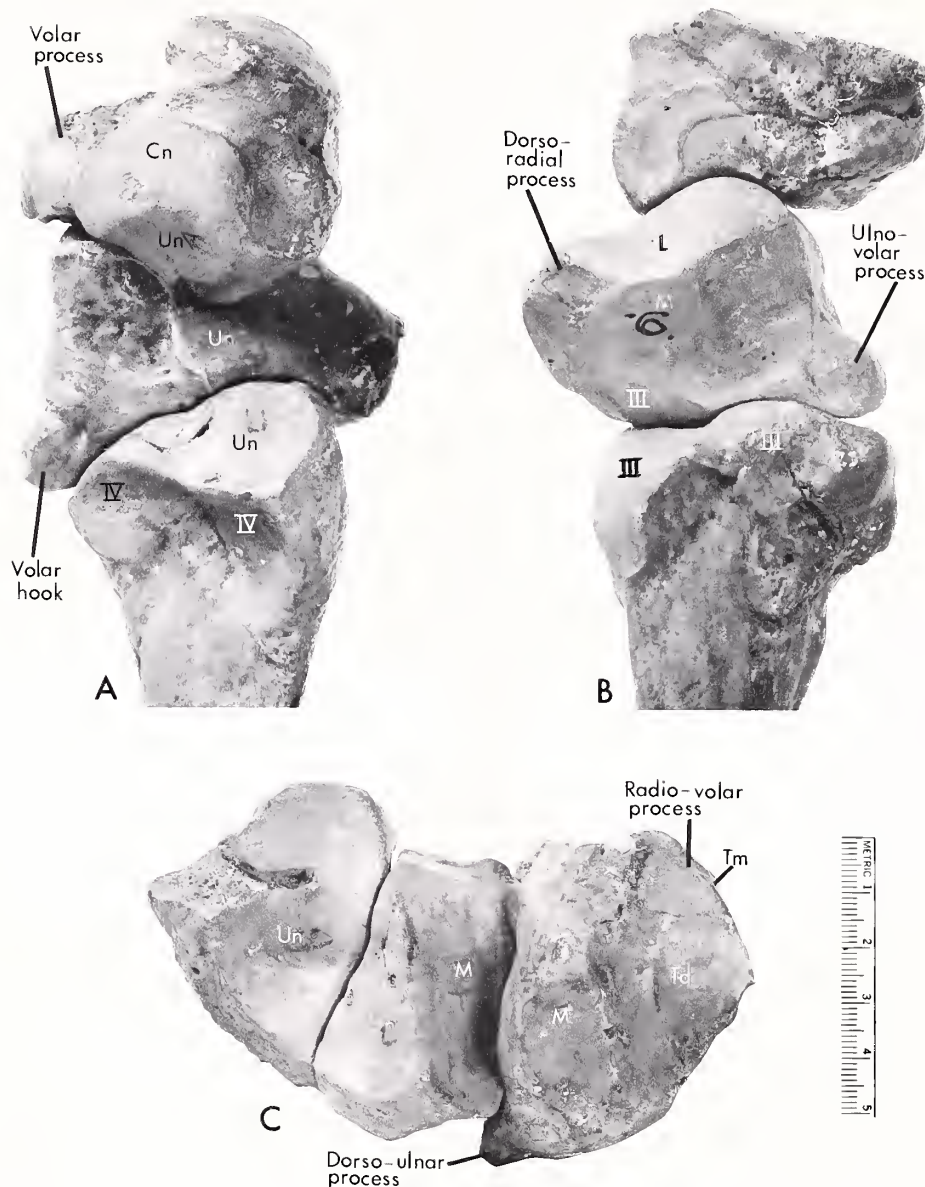


Fig. 12.—A) Ulnar view of right lunate, magnum, and Mc III (dorsal edge at right), B) radial view of right cuneiform, unciform, and Mc IV (dorsal edge at left), and C) proximal view of right Mc IV, Mc III, and Mc II (dorsal edge below, radial edge at right) of *M. elatus*, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska. See Fig. 10 for facet abbreviations.

adjoining edge, each slightly concave, but the ulna facet more so. When placed in articulation with the cuneiform, the pisiform does not occupy the entire pisiform facet on the cuneiform and so may have been capable of some dorsovolar movement against the cuneiform. The part of the pisiform on which the articular facets lie is expanded in all directions, but volar to that region the pisiform is laterally constricted; still farther in the volar direction the pisi-

form is expanded and rugose for muscle attachment, its end slightly curved in the radial direction.

The unciform (hamate) has two prominent processes, a dorsoradial one and an ulnovolar one. Of these, the former is near the proximal edge of the bone and the latter near the distal edge (Figs. 10C, D). There are two facets on the proximal surface (Fig. 10C), the more distal and radial for the lunate and extending onto the above-mentioned dorsora-

dial process. On its radial side (Fig. 12B), this primarily concave facet adjoins the much smaller magnum facet at a right angle; its volar edge borders the cuneiform facet along a blunt ridge. The cuneiform facet is strongly convex in the dorsal to volar direction and curves onto the volar side of the bone (Fig. 8B). This facet is much larger than the corresponding facet on the cuneiform, so that during flexion of the carpus the unciform was able to move considerably with the result that the volar surface of its cuneiform facet was then in contact with the cuneiform. No facets are present on the roughened ulnar surface of the unciform, for Mc V does not articulate with the unciform. On the radial side of the unciform are two facets (Fig. 12B). The proximal one, for the magnum, has a trapezoidal shape and flat surface and lies on a very weak, distally slanted platform, with the radial surface of the unciform roughened and depressed on either side of it. Generally speaking, the platform for the magnum facet is more pronounced in specimens from Morava Ranch Quarry than in those from the Agate Quarries. There is also variably present in *M. elatus* (absent in Fig. 12) a narrow volar extension of the magnum facet adjoining the lunate facet. The trapezoidal magnum facet indistinctly borders the facet for Mc III, which in turn indistinctly borders the Mc IV facet near the distal edge of the radial surface of the unciform (visibility and location of Mc III-Mc IV facet boundaries vary somewhat among specimens). The weak ridge, which appears to separate the Mc III facet from the Mc IV facet, is actually shared by both facets. The Mc III facet varies in its dorsal to volar extent but in any case does not reach as far in the volar direction as does the Mc IV facet, which occupies the distal surface of the ulnovolar process (Fig. 10D).

Although the magnum is one of the largest bones in the carpus, only a small part of it is visible in dorsal view; it is most strongly developed in its volar part. The largest of the four facets visible from the radial side (Fig. 11B) is that for Mc II, irregular in shape and slightly concave. There are two facets for the trapezoid, a larger dorsal one between scaphoid and Mc II facets and passing onto the proximal surface of the magnum, and a smaller oval-shaped volar one also near the proximal edge (it borders proximally parts of both scaphoid and lunate facets). Of the two large curved facets on the proximal surface of the magnum (Fig. 10C), the more dorsal one articulates with the distal process of the scaphoid. Most of the volar part of the prox-

imal surface is occupied by a convex, ball-shaped lunate facet, which fits into the cup of the volar process of the lunate. The dorsal part of the lunate facet curves onto the ulnar surface of the magnum and is separated by only a weak ridge from the unciform facet. Compared with adjoining facets, the unciform facet is small and flat, lying on a low platform (Fig. 12A). It attains the distal edge of the ulnar side of the magnum where it joins the Mc III facet at right angles. The latter facet, on the distal surface (Fig. 10D), is a very elongated facet, passing in the distovolar direction for nearly the entire extent of the well-developed volar hook. The Mc III facet is irregularly concave along most of its length and may be divided by a dorsal to volar directed ridge into moieties of unequal size.

In both proximal and dorsal views (Figs. 10C, 8A), the trapezoid has a triangular appearance, in the former case the apex being the volar angle, in the latter the distal angle which fits into the proximal groove on Mc II. The entire proximal surface (Fig. 10C) is occupied by the scaphoid facet, concave transversely and convex in the dorsal to volar direction. Curving onto the volar surface of the trapezoid (Fig. 8B), this facet merges into the facet for the trapezium, which occupies most of the volar surface and is continuous with trapezium facets on the scaphoid and Mc II. The scaphoid facet also curves onto the ulnar surface of the trapezoid (Fig. 11A), where it borders the two facets for the magnum. The larger dorsal magnum facet has a slight distal slant and a subtrapezoidal shape. Volar to this facet is a rough-surfaced depression, larger than the dorsal facet itself. Only at the extreme proximovolar edge of the dorsal magnum facet, bordering the scaphoid facet, is a small flattened area representing the volar articular facet for the magnum. Separated by a distinct ridge from the dorsal magnum facet is the facet for Mc II. This distal facet, like its counterpart on Mc II, has a V-shape (Fig. 10D), and its radial edge meets the trapezium facet at an acute to right angle on the volar surface of the trapezoid.

A number of trapezium specimens of *M. elatus* are known. This small bone contacts facets on the scaphoid, trapezoid, and Mc II.

Metacarpals.—The “dorsal surface” of Mc II described by Holland and Peterson (1914) is actually a dorsoradial surface (with radiovolar and dorsoulnar processes at either end, see Fig. 12C) when Mc II is placed in articulation with Mc III. For this reason, dorsal of Holland and Peterson is

here called dorsoradial, a term also adopted by Borissiak (1946) and Belyaeva (1954). In dorsoradial view (Fig. 8A) the proximal surface of Mc II is M-shaped, broadened by radiovolar and dorsoular processes that extend to either side of the shaft. Most of the radiovolar process is occupied by a well-developed trapezium facet (Fig. 8B), which is weakly concave and widest in its radial part. The trapezium facet is contiguous to, but separated by, a sharp crest from the concave trapezoid facet, which forms the middle V of the above-mentioned M (Fig. 12C). An ulnar crest, which joins the one between trapezium and trapezoid facets to form the apex of a triangle enclosing the trapezoid facet (Fig. 12C), separates the trapezoid facet from the magnum facet. The magnum facet is the last (ulnar) limb of the M and overhangs the Mc III facet (Fig. 11A), which forms the proximal part of a deep concavity on the ulnar side of the bone. On the volar side of the dorsoular process the Mc III facet curves distally, so that when Mc II and Mc III are articulated, Mc II covers both dorsoradial and proximoradial parts of Mc III. The shaft of Mc II, almost circular in section, is more massive than that of either Mc III or Mc IV. The distal end is rotated clockwise in relation to the proximal end, having an effect in turn on the orientation of the fused proximal and medial phalanges (bearing the large claw) of this digit. General features of the distal end of Mc II are 1) the strongly developed ulnar tubercle proximal to the phalangeal articular surface, 2) the unequal development of the sesamoid facets, the ulnar facet being wider and extending farther distally than the radial facet, 3) the weakness of the keel between the two sesamoid facets, and 4) the presence of a foramen on the radial surface just proximal to the articular facets. YPM 24.632, a distal end of Mc II, which was part of Marsh's type collection of *M. elatus*, shows no special differentiating features from Agate and Morava Ranch Quarry material.

Most of the proximal part of the dorsal surface of Mc III is rugose (Fig. 8A), except for a subtriangular area, which articulates with the dorsoular process of Mc II. This facet is continuous with the Mc II facet on the proximal surface (Fig. 11B, despite the implication by Holland and Peterson, 1914:350, 352, that the two are separate facets). The proximally oriented part of the Mc II facet extends in a dorsal to volar strip across the radial side of the proximal surface. It is delineated only by a faint ridge from the broader magnum facet, which occupies the middle part of the Mc III proximal sur-

Table 3.—Maximum lengths (in mm) and ratios of maximum lengths of metacarpals in individuals of selected chalicotheres species.

Specimens	Mc II	Mc III	Mc IV	Mc II/ Mc III	Mc IV/ Mc III
<i>Moropus elatus</i>					
AMNH 14.378	198	229	200 ^a	0.86	0.87 ^a
CM 1700	164 ^a	188	166	0.87 ^a	0.88
CM 1604 ^b	230	274	221	0.84	0.81
<i>Moropus hollandi</i>					
CM 1424	174	—	—	—	—
FMNH PI3000	178	206	190	0.86	0.92
<i>Schizotherium priscum</i>					
Specimen in Paris ^c	115	130	126	0.88	0.97
<i>Ancylotherium (A.) pentelicum</i>					
AMNH 32504 ^d	234 ^a	279	275	0.84 ^a	0.98
<i>Chalicotherium grande</i>					
CM 2298 ^e	163	198	212	0.82	1.07

^a Approximate measurement.

^b Measurements taken from Holland and Peterson, 1914.

^c An uncatalogued specimen, possibly a composite, from the Phosphorites of Quercy, located in Muséum National d'Histoire Naturelle, Paris.

^d Cast of an uncatalogued specimen from Pikermi in the Muséum National d'Histoire Naturelle, Paris.

^e Cast of specimen from Sansan (Gers), France.

face (Fig. 12C). Along its dorsal to volar axis the magnum facet is concave in its dorsal part and convex in its volar part, extending farther in a volar direction than any other part of the proximal surface. A sharp crest separates the magnum facet from that for the unciform, which adjoins it in the ulnar direction. This latter facet is subtriangular with a volar apex and overhangs the facet(s) for Mc IV, separated by another sharp crest (Fig. 12A). Despite Holland and Peterson's (1914:353) observation of a double Mc IV facet, divided into two by a sinus, there is often a single, undivided facet. In any case the Mc IV facet(s) occupies (-y) the proximal surface of a large concavity on the ulnar surface of Mc III. The shaft of Mc III is subquadrate in section and the distal end is only slightly asymmetrical. A blunt ridge continues distally from the Mc II facet along the dorsoradial angle for about half the length of the shaft.

Mc IV is oriented so that what seems to be a flat dorsal surface (Fig. 8A) actually has a dorsoular orientation when the bone is articulated with Mc III, a situation the opposite of that for Mc II. Of the two Mc III facets (Fig. 12B, or parts of a single,

undivided facet), the largest and most convex is the dorsal one, whereas the smaller volar facet has a less proximal and more completely radial orientation. Separated from the Mc III facet(s) by a weak to somewhat pronounced rib, the unciform facet occupies almost all of the proximal surface of Mc IV and is subtriangular with a volar apex (Fig. 12C). An important feature of Mc IV is its articular surface for Mc V, the reduced metacarpal that articulates with no other bone. This articulation is on the ulnovolar angle of Mc IV (Fig. 8B) and is separated from the proximal edge by paired tubercles (one ulnar, one volar). The Mc V facet is on the distal volar surface of the ulnar tubercle. The shaft of Mc IV becomes more oval and less triangular in section distally. Mc IV is less symmetrical than Mc III, but more so than Mc II, and at its distal end the radial tubercle is larger than and proximal to the ulnar one, whereas the ulnar of the two sesamoid facets is smaller.

In *M. elatus* Mc V has a two-part Mc IV facet on the dorsoradial side of its proximal end and a transversely compressed shaft. Small sesamoid and phalangeal facets are present on the distal end, which reaches the level distally of the proximal end of sesamoid facets in Mc IV. In articulation with Mc IV, Mc V was somewhat volar to the other metacarpals and was strongly divergent at its distal tip from the remainder of the manus.

Manus summary.—A complete analysis of the manus is best taken as part of a broad functional study of *Moropus* (Coombs, in preparation), but a few comments are useful. Despite the lack of rotation ability at the wrist (see radius-ulna comments), carpal facets suggest that the wrist was quite flexible from side to side and that strong flexion was possible along two planes, at the ulnocarpal joint and between the proximal and distal rows of carpals. Manus flexion in *M. elatus* was not so pronounced, however, as in *Ancylotherium* (*Ancylotherium*) *pentelicum* (Schaub, 1943), where the trapezium was lost and the scaphoid could contact Mc II during extreme flexion. Weight was borne primarily by the distal ends of the metacarpals, with participation by the sesamoids and the proximo-volar ends of proximal phalanges. Except for the tips of the ungual phalanges, the hooked digits were probably held clear of the ground during walking by hyperextension of the proximal phalanx and flexion of the other phalanges (see digit II of manus in Fig. 2). Mc III and Mc IV are almost the same length, but weight was concentrated on the more symmet-

rical Mc III. The torsion and other unusual features of the relatively short Mc II are associated with the bearing of the large hooked claw by this digit.

Hindlimb

Innominate.—Complete pelvis specimens are otherwise rare in *Moropus* but are well known in *M. elatus*. Chalicotheres features not shown so strongly in other perissodactyl innominates are the longer and narrower pelvic proportions, primarily because of expansion of the ischium and pubis posterior to the acetabulum and the fairly long shaft of the ilium. Articulation with the femur and relations to the sacrum and lumbar vertebrae suggest that the ilium was nearly vertical in the living animal, although probably not so sharply vertical as it was mounted by Osborn (AMNH 14.375, Fig. 2). On the medial surface of the ilium, the articular surface for the sacrum is heavy and rather long. The iliac crest is expanded but not strongly so. Aside from the rugosities along the iliac crest, there is an obvious rugose area of muscle attachment (for the rectus femoris) just anterior and dorsal to the acetabulum. The acetabulum is deeply excavated with a heavy dorsal overhang, which aided in supporting the body over the femur.

Femur (Fig. 13B).—Holland and Peterson (1914), while describing the femur of *M. elatus*, compared and differentiated it from the femur of titanotheres. Actually the greatest problem in the identification of *Moropus* femora is in comparison with those of rhinoceroses found in beds of the same age, usually in greater numbers. Features, which usually differentiate a *Moropus* femur, are 1) the symmetrical or nearly symmetrical (less symmetrical in older individuals), slightly oblique patellar facet (that in rhinos is more asymmetrical), 2) the asymmetrical development of the distal condyles, the medial condyle extending farther posteriorly (condyles of contemporary rhino femora are more nearly symmetrical), 3) the lesser development of the third trochanter, and 4) the very small but persistent *fovea capitis* on the head for attachment of the *ligamentum teres* (the *fovea* on rhinoceros femora is usually larger).

The large number of known *M. elatus* femora are essentially similar in morphology, although there is some individual variation in the proportional width of the shaft. In larger femora of *M. elatus*, the shaft is relatively broader. Weight-bearing adaptations such as this, in a species where size variation is as great as in *M. elatus*, suggest that one must be care-



Fig. 13.—Anterior views of A) distal end and shaft of left humerus, B) right femur, C) patella, and D) left tibia of *M. elatus*, AMNH 14.378, from the Agate Spring Quarries, Sioux Co., Nebraska. Abbreviations: D.r., deltoid ridge; C.f., coronoid fossa; Cap, capitulum; Ent, entepicondyle; Ect, ectocondylar ridge; 1, greater trochanter (broken); 2, lesser trochanter; 3, third trochanter; Pat, patellar facet; Cnm, cnemial crest; Mm, medial malleolus; F, fibula articulations.

ful in drawing specific boundaries on the basis of proportions alone. In addition to the characters cited above, *M. elatus* femora share well-developed greater and lesser trochanters and a fairly deep trochanteric fossa. Distal to the third trochanter, the shaft narrows quite abruptly and then broadens close to the distal end.

Tibia and fibula.—Among known *Moropus* species, the fibula has been preserved only in *M. elatus*; it will not be discussed further here. Tibiae vary little in proportions and morphology, and there is therefore little to add to the description of Holland and Peterson (1914:363). Some of the most prominent features are (Fig. 13D): 1) a heavy cnemial crest, which is rugose proximally and extends a good distance distally along the shaft, 2) two broad

proximal articular surfaces for the condyles of the femur, of which the lateral surface is slightly more curved, 3) a V-shaped or double (spreading apart anteriorly) spine between the two femur articular surfaces, with the medial side of the spine sharper and taller, 4) well-developed articular surfaces both proximolaterally and distolaterally for the fibula and a well-defined ridge for the interosseous ligament connecting the proximal and distal facets, and 5) a strong medial malleolus. There is no evidence that the medial malleolus contacted the calcaneum during extreme flexion as Holland and Peterson suggested.

Patella (Fig. 13C).—Patellae are not known for all *Moropus* species, but there is some evidence of differences among species. Patellae of *M. elatus*

Table 4.—Measurements (in mm) of astragali of selected chalicotheriid specimens, including proportions of tibial height/maximum width.

Taxa and specimens	Maximum width	Height of tibial side ^a	Height/width
<i>Moropus elatus</i> , AMNH 14378 ^b	89.9	74.7	0.83
<i>Moropus elatus</i> , CM 1701 ^b	76.7	68.8	0.86
<i>Moropus elatus</i> , AM 9722 ^c	89.7	68.8	0.77
<i>Moropus elatus</i> , AM 9723 ^c	92.9	74.5	0.80
<i>Moropus elatus</i> , AM 9724 ^c	90.8	71.2	0.78
<i>Moropus elatus</i> , Range of six Frick Morava Ranch Quarry specimens	81.1–98.0	62.5–77.2	0.77–0.82
<i>Moropus hollandi</i> , CM 1424 ^d	84.1	64.0	0.76
<i>Moropus hollandi</i> , F:AM 54,902g	103.5	74.4	0.72
<i>Moropus merriami</i> , UCMP 11,605	100.7	64.9	0.64
<i>Moropus merriami</i> , UCMP 19,404	102.6	62.2	0.61
<i>Schizotherium turgaicum</i> ^e	43.5	38.5	0.89
<i>Schizotherium turgaicum</i> ^e	47	41	0.87
<i>Borissiakia</i> <i>betpakdalensis</i> ^f	92	74	0.80
<i>Borissiakia</i> <i>betpakdalensis</i> ^f	68	58	0.85
<i>Ancylotherium</i> (<i>Metaschizotherium</i>) <i>fraasi</i> ^g	83.4	56.0	0.71
<i>Chalicotherium</i> <i>rusingense</i> ^h	66.0	35.7	0.54
<i>Chalicotherium salinum</i> , AMNH 19,436	88.6	37.7	0.43
<i>Chalicotherium grande</i> , CM 2299 (cast)	100.7	41.2	0.41
<i>Chalicotherium grande</i> ^h	100.5	46.2	0.46
<i>Chalicotherium goldfussi</i> ^h	98.7	44.7	0.45

^a Height measurement includes neck and edge of navicular facet.

^b From Agate Spring Quarries, Sioux County, Nebraska.

^c From Morava Ranch Quarry, Box Butte County, Nebraska.

^d Holotype, right side.

^e Taken from Belyaeva, 1954:57–58.

^f Taken from Borissiak, 1946.

^g Taken from von Koenigswald, 1932.

^h Taken from Butler, 1965.

have 1) the facet for femur not so wide transversely as tall, 2) the trochlear ridge between the two sides of the femur facet blunt, with curved sides of the facet at obtuse angles to one another, 3) the anterior

patellar surface rugose with some but not strong development of a proximal ridge for the insertion of knee extensors, and 4) a distal tongue developed at the patellar apex (except in one Morava Ranch Quarry specimen). It is important to note that YPM 24,632, a patella, which was part of Marsh's type collection of *M. elatus* and first figured by Holland and Peterson (1914:223), is like the majority of patellae of *M. elatus*.

Tarsals (Figs. 14–17).—In all astragali of *M. elatus* a small neck distal to the trochlea is present (Fig. 14C), on whose distal surface the large navicular facet lies. The neck is most pronounced on the tibial side of the bone, in some specimens very pronounced, but it may be reduced at its fibular edge (distal to the middle part of the astragalar trochlea). Over half the width of the astragalus is occupied by the fibular side of the trochlea, which is more gradually slanted than the tibial side. The fibular edge of the trochlea does not ascend proximally quite so far as does the tibial edge, and distally it hangs free from the rest of the bone (but does not extend farther distally than the navicular facet). On the volar surface of the astragalus (Fig. 14B), the most obvious feature is the deeply concave ectal facet for the calcaneum, which extends more than half the transverse width of the astragalus as well as over half the height. The ectal facet is rather uniformly concave from proximal to distal throughout its width. A sharp proximal ridge separates the ectal facet from the dorsal surface of the trochlea. Distally, across a blunt ridge along the fibular half of its width, the ectal facet borders the smaller, weakly convex calcaneal facet, also for the calcaneum. The latter facet is slanted strongly in a distal direction and away from the ectal facet. Both ectal and calcaneal facets are separated by a rugose area containing nutrient foramina from a third facet for the calcaneum, the sustentaculum, on the tibio-distal side of the astragalus' volar surface. The sustentaculum facet is generally oval in shape, weakly convex, and lies flat on the plane of the volar surface. On the distal surface of the astragalus the single facet for the navicular is distinctly pear-shaped with a narrow fibular end. Weakly convex transversely and at its fibulovolar angle, the facet passes slightly onto the fibular and volar surfaces of the astragalus, but along its entire dorsal edge a distinct ridge separates it from the dorsal surface.

The tuber calcis of the calcaneum is long and massive, with a subtriangular cross-section. Its dorsal surface is narrower than its rugose volar surface,

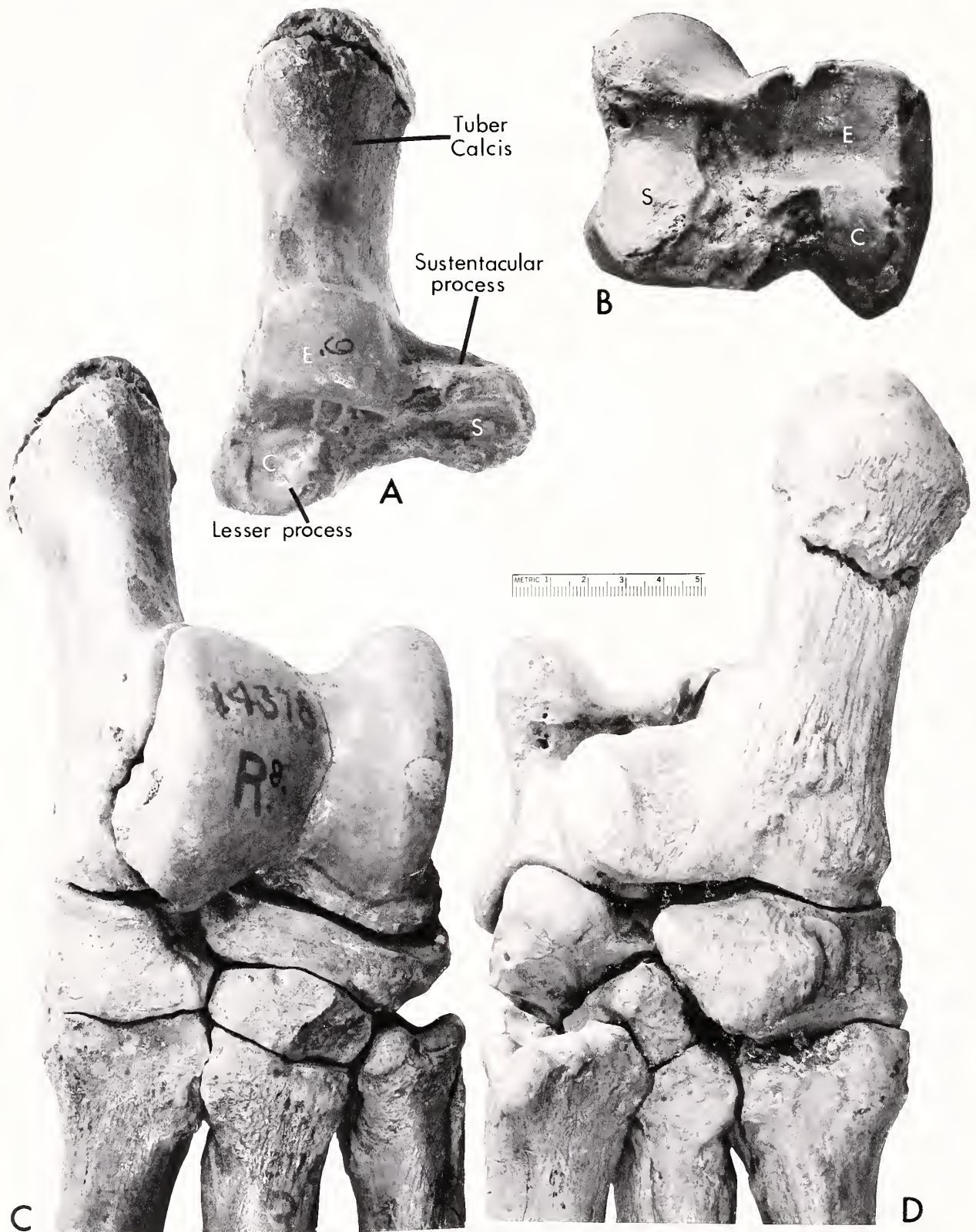


Fig. 14.—A) Dorsal view right calcaneum, B) volar view right astragalus, C) dorsal view right tarsus, and D) volar view right tarsus of AMNH 14,378 (missing mesocuneiform and entocuneiform), *M. elatus*, from the Agate Spring Quarries, Sioux Co., Nebraska. Tarsus elements identified in Fig. 15; facets on astragalus and calcaneum abbreviated as follows: E, ectal; S, sustentacular; C, calcaneal.

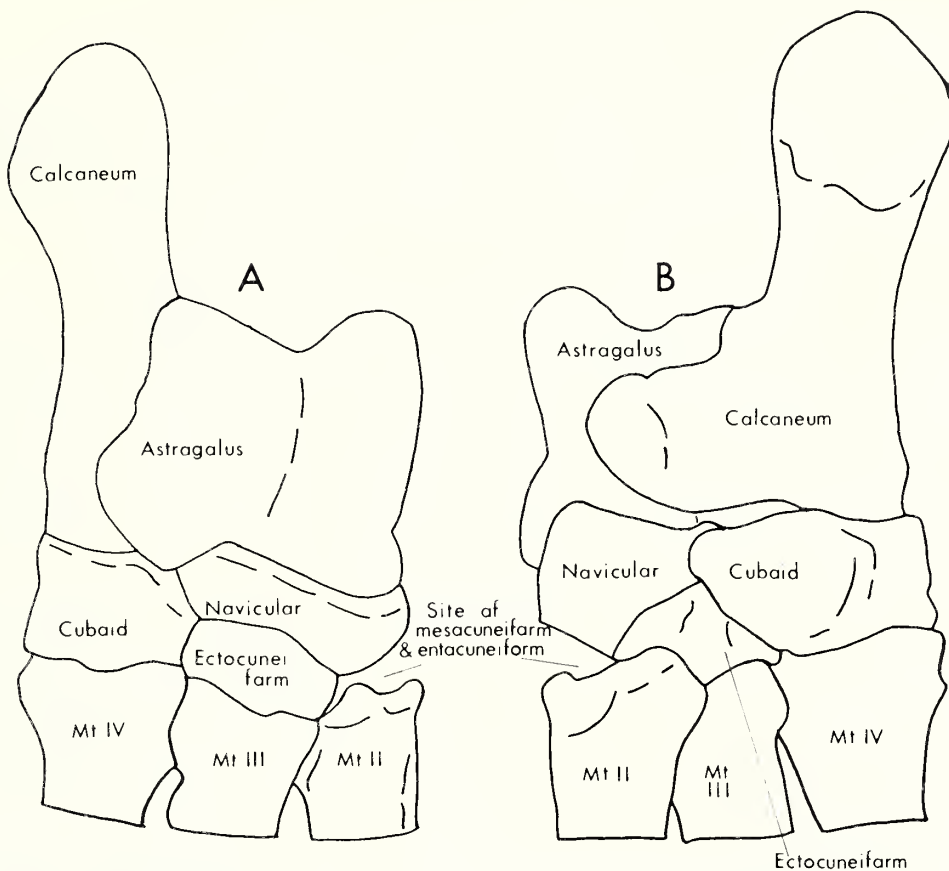


Fig. 15.—Labeled drawing of dorsal and volar views of tarsus of AMNH 14,378 shown in Fig. 14.

and the end of the tuber, where there is a pronounced rugose area for muscle attachment particularly characteristic of this species (Fig. 14D), is thicker than the shaft. Of the facets for the astragalus (Fig. 14A), the ectal facet is relatively narrow but extends well onto the dorsal surface of the tuber. Here it is only weakly convex, but distal to the tuber it forms a protruding right-angle bend corresponding to the deeply concave ectal facet on the astragalus. On some specimens there appears to be a facet for the tibia at the edge of the ectal facet on the tuber (mentioned by Holland and Peterson, 1914:366, although no particular evidence for it exists on the tibia). In those specimens where such a facet exists, the ectal facet, rather than being flat on the tuber, is raised on a platform so that the tibia facet is continuous with the astragalar trochlea when the astragalus and calcaneum are articulated [also noted in *Ancylotherium* (*A.*) *pentelicum*]. The oval, slanted sustentacular facet occupies almost the entire sustentacular process and is separated

from the ectal facet by a groove for the interosseous ligament. The third facet, corresponding to the calcaneal facet on the astragalus, is distal to the ectal facet on what Holland and Peterson termed the "lesser process," which is well developed. On the distal end of the calcaneum is the pear-shaped cuboid facet, flat on its fibular side and slightly concave on its tapering tibial side. There is no facet on the narrow distal surface of the sustentacular process. The paralectotype of *M. elatus*, YPM 24,631, includes a broken calcaneum. Although retaining only the tuber calcis, it can without question be connected with the other specimens here described. Important common features are the strong rugose protuberance at the end of the tuber calcis and the shape of the ectal facet as it extends onto the tuber.

On the cuboid, the calcaneum facet is pear-shaped (Fig. 16E), corresponding exactly to the distal facet on the calcaneum. It occupies the entire proximal surface and is set off by a ridge from the remainder of the bone; articulation with the calca-

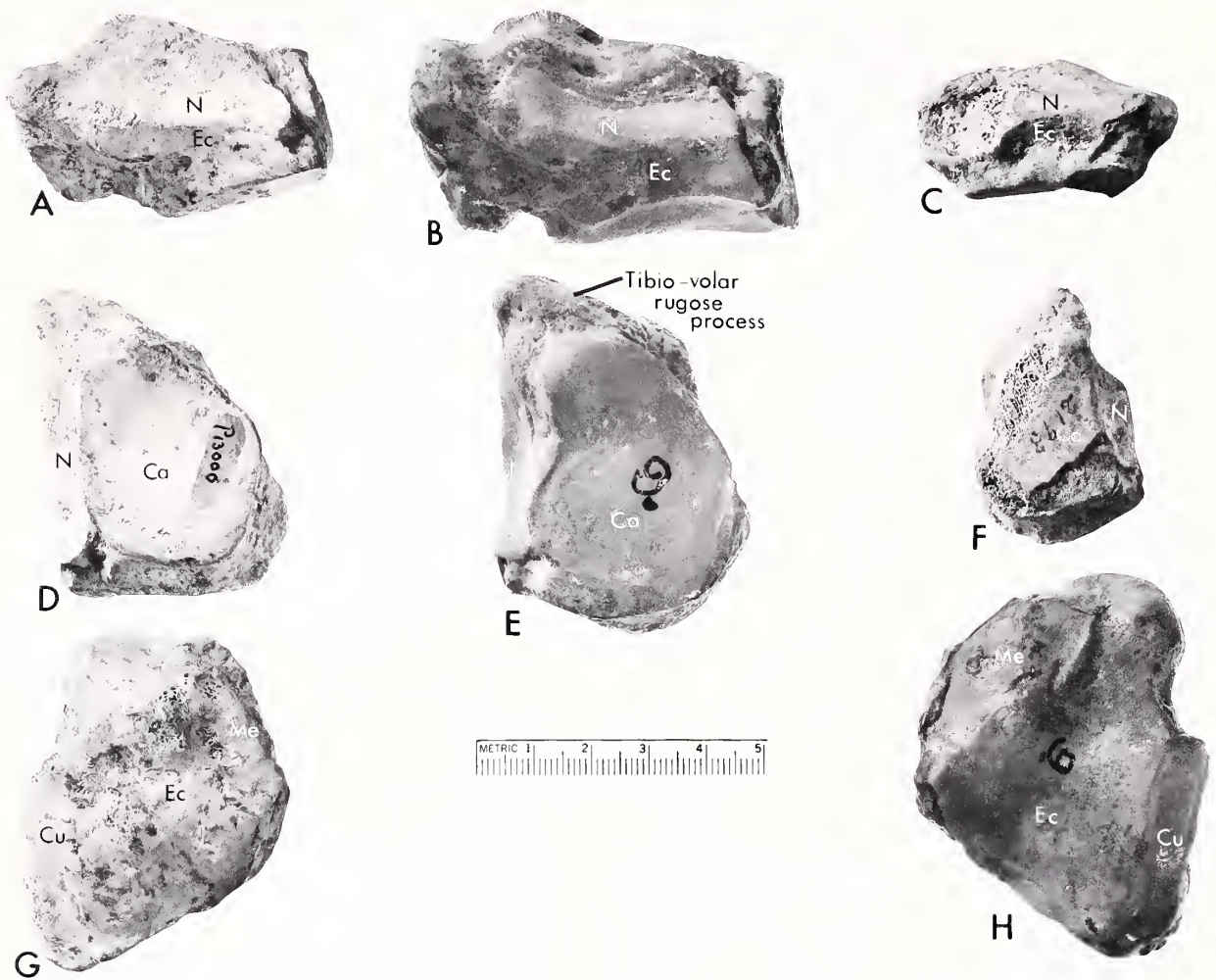


Fig. 16.—Tibial (A - C, proximal edge at top) and proximal (D - F, dorsal edge at bottom) views of cuboids of *M. hollandi* (A, D, left cuboid), FMNH P13000, from near Jay Em, Goshen Co., Wyoming; *M. elatus* (B, E, left cuboid), AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska; and *M. distans* (C, F, right cuboid), YPM 24,628, from Bridge Creek, Oregon. Distal views (dorsal edge at bottom) of naviculars of G) *M. hollandi*, FMNH P13000, and H) *M. elatus*, AMNH 14,378. Facet abbreviations used in Figs. 16-19 and 27-28 are as follows: Ca, calcaneum; Cu, cuboid; N, navicular; Ec, ectocuneiform; Me, mesocuneiform; II, Mt II; III, Mt III; IV, Mt IV.

neum is slightly oblique. The dorsal, fibular, and most of the volar surfaces of the cuboid are gently curved and relatively smooth, but at the tibio-volar angle is developed a strongly rugose process for muscle attachment, which overhangs Mt IV (Figs. 14D, 16B, 17C). The tibial side of the cuboid (Figs. 16B, 17C) has no articular surface in its most proximal and volar parts, where it is separated from the navicular by a small space. The navicular facet lies in a dorsal to volar strip, which occupies one-third of the height of the tibial surface and lies about halfway between the proximal and distal edges of the bone. This facet is slanted to form the proximal

part of a V of which the ectocuneiform facet is the distal part. Occupying the most distal part of the tibial surface, the ectocuneiform facet consists of dorsal and volar divisions, which may or may not be separate. The distal surface of the cuboid, except for the tibio-volar process, is occupied by the large quadrilateral facet for Mt IV, weakly concave except near its tibio-volar angle where it is convex.

The proximal facet of the navicular is transversely concave, particularly at its tibio-volar angle, where it follows the curve of the corresponding facet on the astragalus (Figs. 14C, 17B). Three other facets are visible on the distal surface (Figs. 16H,

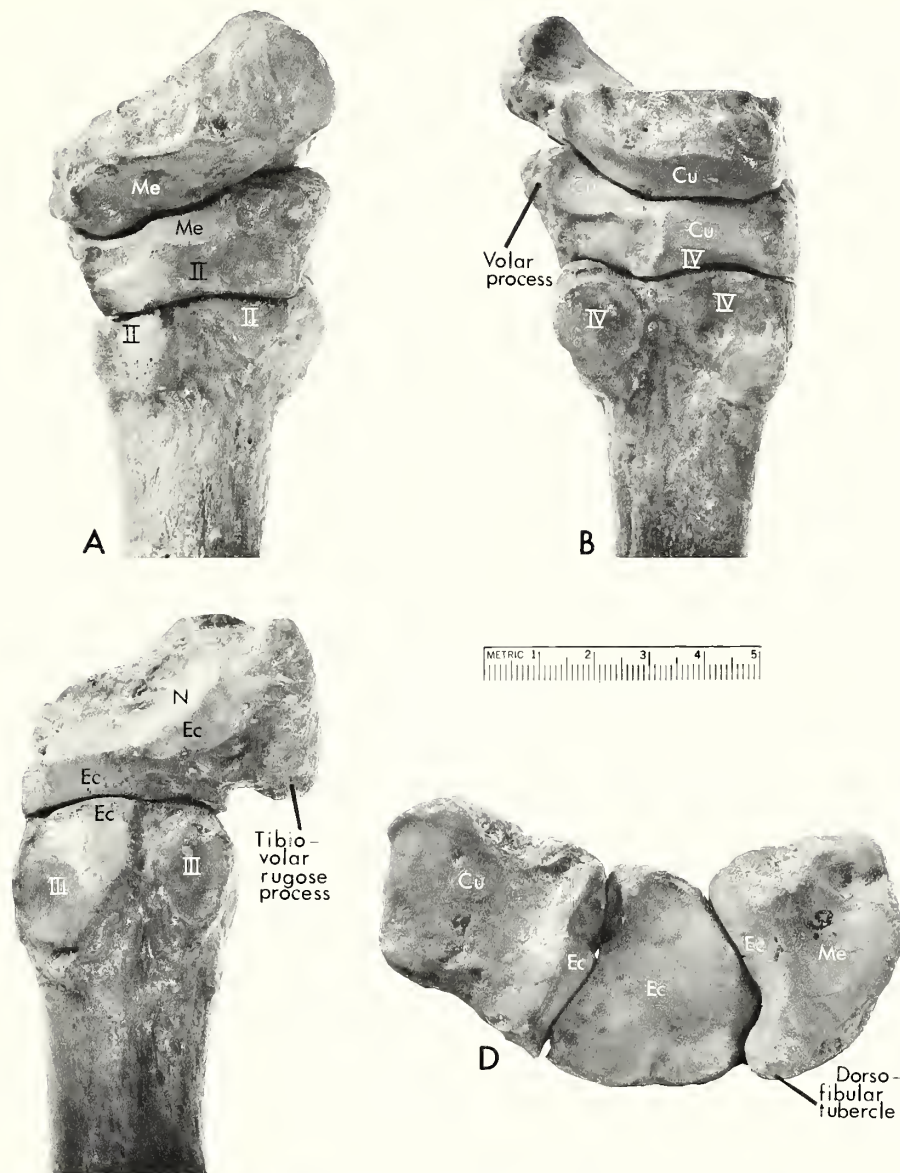


Fig. 17.—Views of right tarsals and metatarsals of *M. elatus*, AMNH 14,378, from the Agate Spring Quarries, Sioux Co., Nebraska: A) Tibial view of navicular, ectocuneiform, and Mt III (dorsal edge at left); B) fibular view of navicular, ectocuneiform, and Mt III (dorsal edge at right); C) tibial view of cuboid and Mt IV (dorsal edge at left); D) proximal views of Mt IV, Mt III, and Mt II (dorsal edge at bottom). Facet abbreviations as in Fig. 16.

17A, B). Of these, the cuboid facet (fibularmost) does not abut the astragalus facet and is like a short dorsal to volar bar (like the corresponding facet on the cuboid). The ectocuneiform facet is about two times as large as that for the mesocuneiform (the most tibial of the distal facets) and has an irregular surface (primarily convex in a dorsal to volar direction) and shape (broadest dorsally and tapering in the volar direction). A shallow groove near the vo-

lar edge of the ectocuneiform facet to accommodate a weak ridge of the ectocuneiform prevents dorsal to volar movement of the navicular and ectocuneiform against one another. The irregularly curved, weakly convex mesocuneiform facet is slanted to approach on its tibial side, but not adjoin, the facet for the astragalus. Weak ridges between the three distal facets of the navicular are their only distinguishing boundaries.

Table 5.—Maximum lengths (in mm) of the three metatarsals within single chalicotheriid specimens.

Specimens or taxa	Length Mt II	Length Mt III	Length Mt IV	Mt II/ Mt III	Mt IV/ Mt III
AMNH 14378 ^a	133.7	146.4	148.3	0.91	1.01
CM 1701 ^a	109.9	124.9	126.8	0.88	1.01
CM 1706a ^a	134	156	157	0.86	1.01
F:AM 54903 ^b	—	115.7	129.8	—	1.12
<i>Schizotherium priscum</i> ^c	95	118	116	0.81	0.98
<i>Ancylotherium</i> (A.) <i>pentelicum</i> ^d	127.0	171.3	147.2	0.74	0.86
<i>Chalicotherium grande</i> ^e	65.8	77.7	107.7	0.85	1.39

^a Specimens of *Moropus elatus* from the Agate Spring Quarries, measurements of CM 1706a from Holland and Peterson, 1914.

^b *Moropus* cf. *M. hollandi*.

^c Specimen (possibly a composite) from the Phosphorites of Quercy in the Muséum National d'Histoire Naturelle, Paris.

^d AMNH 10,564, cast of specimen from Pikermi in the Muséum National d'Histoire Naturelle, Paris.

^e CM 2299, cast of specimen from Sansan.

On the proximal surface of the ectocuneiform, the shield-shaped navicular facet is broadest dorsally and occupies all except the volar angle of the bone, where there is a well-developed, rugose volar process (Figs. 14D, 17B). This process closely approaches the larger tibiovolar process of the cuboid when ectocuneiform and cuboid are articulated. There are some differences among ectocuneiform specimens in proportions and in the development of a single or double cuboid facet on the fibular surface. An important feature on the dorsal part of the fibular surface (Fig. 17B), distal to the cuboid facet(s), is a rounded facet for Mt IV, very distinct and continuous with the cuboid facet(s). On the tibial side of the ectocuneiform lie two articular surfaces (Fig. 17A). The proximal one, for the mesocuneiform, is small and flat. It occupies the middle third of the dorsal to volar depth of the ectocuneiform and is delineated from the proximal surface of the bone by a sharp ridge. Distal to this facet and occupying the entire depth of the ectocuneiform is the band-like, slightly convex facet for Mt II. Thus the ectocuneiform of *M. elatus* contacts all three metatarsals. On its distal surface is an irregularly shaped and generally flat articular surface for Mt III, occupying all except the most volar part of the bone.

The mesocuneiform is a small bone with a slightly concave navicular facet covering most of its proximal side. The slightly convex facet for Mt II oc-

cupies the volar two-thirds of the distal surface. There is also a small articular facet on the tibial side of the mesocuneiform, probably for an entocuneiform. No entocuneiform has been shown for any *Moropus* species, but apparently a small remnant of the bone was present. It did not articulate with Mt II, and there is no sign of an articulation for it on any naviculars examined. The presence of an entocuneiform in *M. elatus*, as well as in *Ancylotherium* (A.) *pentelicum* where a facet for it is also known on a mesocuneiform specimen (a specimen in the Muséum National d'Histoire Naturelle, Paris, casted as AMNH 10,564), is in disagreement with a statement by Radinsky (1963:7) that the entocuneiform was lost in the Chalicotheriidae. The entocuneiform facet has only a small dorsal to volar extent in *M. elatus*.

Metatarsals (Figs. 14–15, 17–19, 27).—Metatarsal proportions provide an important means of separating certain *Moropus* species, for there was apparently an increase over time in width relative to length. Proportions and other morphological features are fairly consistent within a single species, even despite variations in absolute size (Table 6). Thus where intraspecific variation can be evaluated, a metatarsal or other foot element can provide a very useful characterization of a species. For this reason a metatarsal (YPM 13,081, Mt II) was chosen as *M. elatus* lectotype from among the type material mentioned by Marsh (1877). Mammalian feet are often considered too plastic for detailed taxonomic work, but at least in *Moropus* such a restriction does not seem to apply, possibly because of rapid evolution of and strong selection on the manus and pes while the dentition remained relatively plastic within species and constant between species.

YPM 13,081, the Mt II chosen as the lectotype, corresponds closely in proportions and morphology to specimens from both the Agate Quarries and Morava Ranch Quarry (Fig. 18). There is some variation among Mt II specimens in the size and shape of the concave mesocuneiform facet, which occupies the proximal surface (Fig. 17D). In some (YPM 13,081 and the Morava Ranch Quarry specimens) the facet has a greater dorsal to volar extent and accompanies the ectocuneiform facet to the volar edge, separated from the latter facet by a blunt projection. In others (primarily Agate Quarry specimens) the mesocuneiform facet does not extend so far in the volar direction and is more separated in its volar part from the ectocuneiform facet. The sin-

Table 6.—Length and width (in mm) of metatarsals of selected schizotheriine species, with proportions of width versus length.

Species and specimens	Greatest length	Greatest distal width	Minimum shaft width	Length/distal width	Length/shaft width
<i>Mt II</i>					
<i>Moropus elatus</i> AMNH 14,378 ^a	133.7	41.6	26.6	3.2	5.0
<i>Moropus elatus</i> CM 1701	109.9	30.4	18.9	3.6	5.9
<i>Moropus elatus</i> YPM 13,081 (lectotype)	136.2	36.4	26.2	3.7	5.2
<i>Moropus elatus</i> F:AM 54,447 ^b	137.1	38.3	24.5	3.6	5.5
<i>Moropus elatus</i> (range three Frick specimens ^b ; mean three Frick specimens ^b)	109.3–139.5 120.0	30.4–37.5 33.6	20.9–22.3 21.6	3.4–3.7 3.6	5.1–6.25 5.5
<i>Schizotherium priscum</i> (see specimen in Table 5)	95	19	15	5.0	6.3
<i>Ancylotherium</i> (A.) <i>pentelicum</i> (see specimen in Table 5)	127.0	52.3	38.1	2.4	3.3
<i>Mt III</i>					
<i>Moropus elatus</i> AMNH 14,378 ^a	146.4	44.3	28.9	3.3	5.1
<i>Moropus hollandi</i> FMNH P13000	130.7	39.4	28.4	3.3	4.6
<i>Moropus</i> cf. <i>M. hollandi</i> F:AM 54,903	115.7	43.3	30.4	2.7	3.8
<i>Schizotherium priscum</i> (see specimen in Table 5)	118	24	23.2	4.9	5.1
<i>Ancylotherium</i> (A.) <i>pentelicum</i> (see Table 5)	171.3	61.9	47.1	2.8	3.6
<i>Mt IV</i>					
<i>Moropus elatus</i> AMNH 14,378 ^a	148.3	43.9	28.2	3.4	5.3
<i>Moropus elatus</i> CM 1701 ^a	126.8	34.9	23.2	3.6	5.5
<i>Moropus elatus</i> AM 9955 ^b	158.7	51.2	36.0	3.1	4.4
<i>Moropus elatus</i> (range five Frick specimens ^b ; mean five Frick specimens ^b)	123.9–164.8 149	35.7–45.2 41	26.0–31.9 29	3.5–3.8 3.6	4.8–5.4 5.1
<i>Moropus</i> cf. <i>M. hollandi</i> F:AM 54,903	129.8	38.5	27.5 ^c	3.4	4.7 ^c
<i>Moropus</i> sp. (St.-Gérard) (see Coombs, 1974)	88.9	28.0	19.8	3.2	4.5
<i>Schizotherium priscum</i> (see specimen in Table 5)	116	22	28	5.3	4.7
<i>Ancylotherium</i> (A.) <i>pentelicum</i> (see Table 5)	147.2	59.3	45.3	2.5	3.2

^a From the Agate Spring Quarries.^b From Morava Ranch Quarry.^c Approximate measurement.

gle ectocuneiform facet at the fibular edge of the proximal surface has a primarily fibular, but slightly proximal, orientation (Fig. 18D). In some specimens the area connecting the dorsal and volar parts of this facet is slightly constricted. Distal to the ec-

tocuneiform facet and adjacent to it is a small Mt III facet, whose dorsal and volar parts are connected only by a very narrow band at the facet's proximal edge. A dorsofibular tubercle at the proximal end of all the Mt II specimens helps to prevent

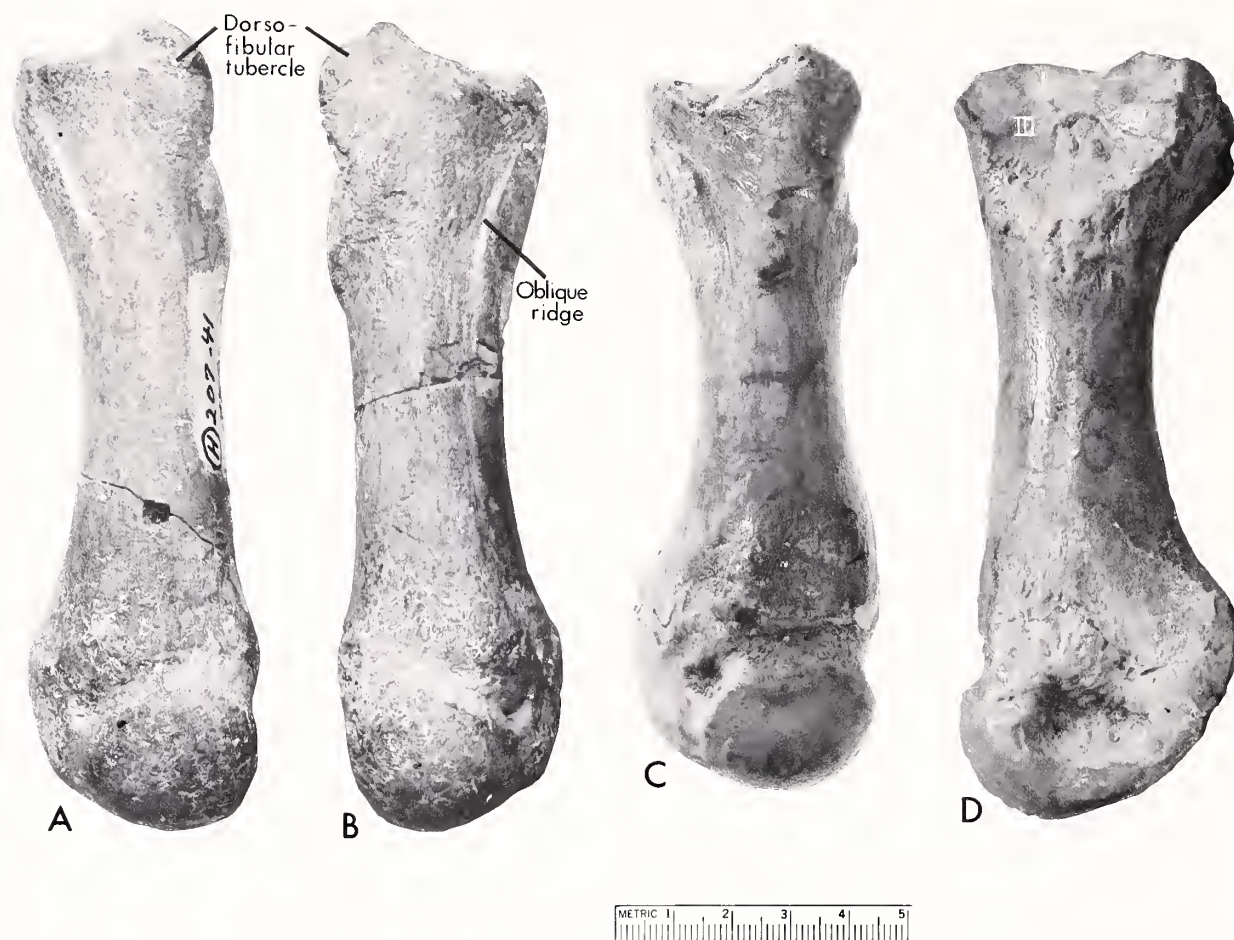


Fig. 18.—Dorsal views of A) left Mt II of F:AM 54.447, *M. elatus*, from Morava Ranch Quarry, Box Butte Co., Nebraska; B) right Mt II of YPM 13.081, lectotype of *M. elatus*; C) left Mt II of AMNH 14.378, *M. elatus*, from the Agate Spring Quarries, Sioux Co., Nebraska; D) Fibular view of left Mt II of AMNH 14.378. Facet abbreviations as in Fig. 16.

any dorsal to volar movement of Mt II against the ectocuneiform or Mt III. A depressed area on the fibular surface bordering the Mt III facet is succeeded distally by a strongly rugose area. Very characteristic of this bone is an oblique longitudinal ridge for muscle insertion along the tibiodorsal angle of the proximal part of the shaft; this ridge is more distinct in some specimens than in others. The distal end of Mt II is slightly asymmetrical.

The proximal end of an Mt III of YPM 24.631, a paralectotype of *M. elatus* (see Fig. 19A, B), is indistinguishable from other referred Mt III specimens but probably belonged to a larger individual than the Mt II considered as the lectotype. On each Mt III specimen, the ectocuneiform facet, on the proximal surface, is rather flat and slanted distally toward the tibial side (Figs. 17D, 19A). The shape of the proximal end of the bone is subtriangular with

the ectocuneiform facet occupying practically all of this surface. On the tibial side of the bone (Figs. 17A, 19A) the small articular surface for Mt III is bipartite with dorsal and volar parts connected by a very narrow strip of articular surface (the connection may be absent in some specimens). Sometimes the dorsal part of the facet is larger, sometimes the volar, and sometimes the parts are subequal. The two facets for Mt IV, on the fibular side of the proximal end (Figs. 17B, 19B), are large compared to the Mt II facet. In some specimens the dorsal and volar facets are distinctly separated by an intervening sharp depression; in others they are directly adjacent though not confluent. In all the specimens examined, the dorsal Mt IV facet is easily the larger (about twice as large as the volar facet), and both facets are flat to slightly concave and slanted slightly toward the center of the fibular

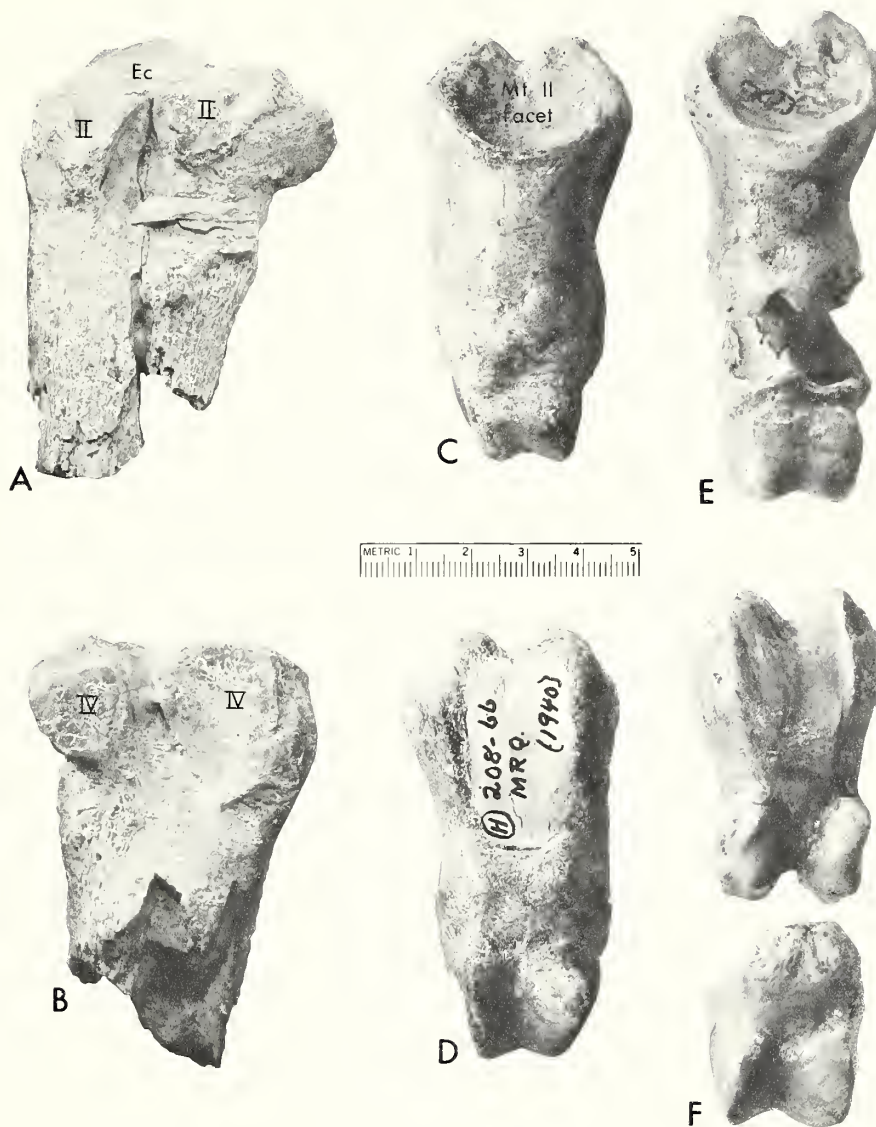


Fig. 19.—Tibial (A) and fibular (B) views of proximal end of Mt III of YPM 24.631, a paralectotype of *M. elatus*. Dorsal (C) and volar (D) views of rare fused proximal and medial phalanges of digit II of the pes of *M. elatus*, F:AM 54.444, from Morava Ranch Quarry, Box Butte Co., Nebraska. Dorsal (E) and volar (F) views of unfused proximal and medial phalanges of digit II of the pes of *M. elatus*, AMNH 14.378, from the Agate Spring Quarries, Sioux County, Nebraska. Facet abbreviations on Mt III as in Fig. 16.

surface (probably restricting dorsal to volar movement between Mt III and Mt IV). Distal to the articular surfaces, rugosities are present on the tibial, volar, and fibular surfaces of the shaft. At the distal end of Mt III the phalangeal articulation is roundly convex and laterally symmetrical, separated dorsally by a depression from the shaft of the bone. There are strong lateral tubercles and a prominent but not sharp keel between the sesamoid facets.

In all examined specimens of Mt IV the proximal head is of quadrilateral shape, slightly wider trans-

versely than deep. The proximal surface (Fig. 17D) is occupied almost entirely by the flat to slightly concave cuboid facet, which is separated by the facets on the tibial side of the bone by a sharp dorsal to volar ridge. The proximal end of the tibial surface has two oval-shaped facets for Mt III (Fig. 17C), of which the dorsal is about twice as large as the volar. The two articular platforms are separated from each other by a groove, and the area just distal to the facets is very rugose. Part of the dorsal facet faces in a dorsal as well as a tibial direction. When Mt IV

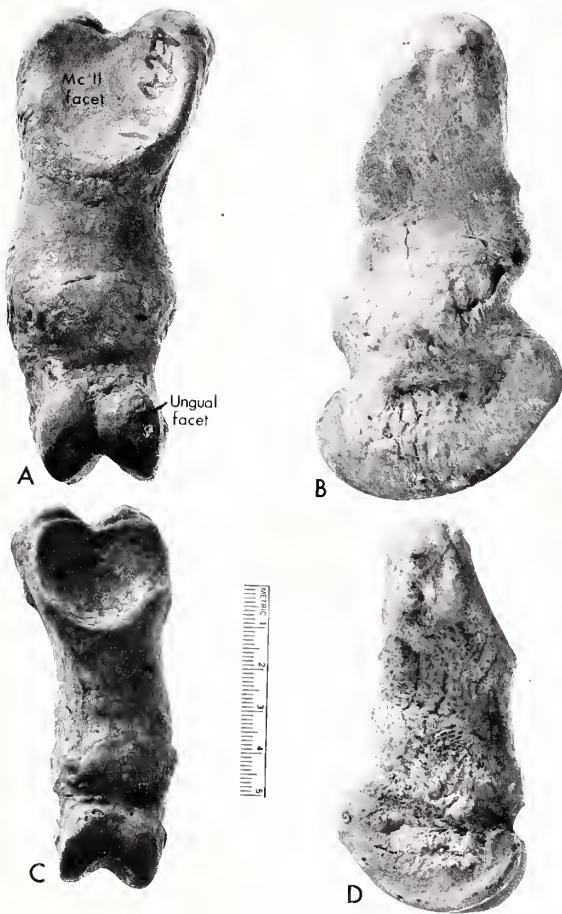


Fig. 20.—Dorsal (A, C) and ulnar (B, D) views of the duplex of digit II of the manus of a presumed male (A, B) of *M. elatus*, AMNH 14.427, left side, and presumed female (C, D) of *M. elatus*, AMNH 14.425, right side, both from the Agate Spring Quarries, Sioux Co., Nebraska.

is articulated with Mt III, the contact between the two bones occupies almost all of the volar facet on Mt IV but only the distal three-fourths of the dorsal facet. The remainder of the dorsal facet articulates with the distal fibular edge of the ectocuneiform (Figs. 17C, D). There are no facets on the fibular surface of Mt IV, but the fibular-volar angle of the proximal end is enlarged and appears to overhang the shaft because of some dorsal to volar compression of the shaft's fibular side. The proximal head and distal end of Mt IV are each rotated in a different direction relative to the proximal part of the shaft axis. On the slightly asymmetrical distal end, the tibial lateral tubercle is stronger than the fibular one, and the tibial side of the phalanx articulation extends farther distally.

Pes summary.—Movement in the pes of *M. elatus* is more restricted than that in the manus, and the pes as a whole is less divergent than the manus from that of other tridactyl perissodactyls. Flexion and extension of the pes occurs primarily at the joint between the tibia and astragalus; most of the joints among tarsals and between tarsals and metatarsals are restricted in size and have stops especially to prevent dorsal to volar flexion. A small degree of side to side movement is possible, however.

The relatively large number of associated specimens permit the observation that Mt III and Mt IV were subequal in length in *M. elatus* and that both were longer than Mt II (Table 5). Consistent with this emphasis on both Mt III and Mt IV, the ectocuneiform articulates with Mt IV as well as Mt III so that weight is spread on both digits (the ectocuneiform also has some articulation with Mt II). In *Ancylotherium* (*Ancylotherium*) *pentelicum* (specimen in Muséum National d'Histoire Naturelle, Paris, figured by Gaudry, 1862), Mt III is clearly the longest digit, and there is no contact between the ectocuneiform and Mt IV. Mt IV in *M. elatus* was also capable of some movement in the fibular direction relative to the rest of the pes; during such movement its contact with the ectocuneiform was lost and its ectocuneiform facet then articulated with Mt III. Metatarsals are much shorter than metacarpals of the same animal.

Phalanges of the pes are similar in structure to those of the manus and were presumably capable of roughly the same movements. They are, however, smaller, and there is no special enlargement of the phalanges of digit II of the pes.

Proximal Phalanges

In *M. elatus*, morphology of phalanges does not differ markedly from digit to digit, except for the distinctive phalanges belonging to digit II of the manus and pes. Thus an isolated phalanx cannot easily be referred to a particular digit or even to the manus or pes, especially when one considers the great size variation among individuals (Coombs, 1975). Nevertheless, certain generalizations concerning the phalanges are possible.

Digit II manus (Fig. 20).—A large, fused proximal and medial phalanx of digit II of the manus is a characteristic feature of *Moropus*. Described as a duplex by Holland and Peterson (1914:357–359), such a bone is present, though broken, among the paralectotypes of *M. elatus* (YPM 24.631, figured

by Holland and Peterson, 1914:223). In juvenile individuals the two bones were not yet fused or were incompletely fused, but in at least one old individual (UCMP 14,377, originally AMNH 14,377, Fig. 21) the ungual phalanx is also fused to the duplex. The angle of fusion in the latter specimen may suggest the usual hooked position of these phalanges during life. Characteristic of the duplex of the manus is the strongly dorsal orientation of the facet for Mc II. The Mc II facet is roughly heart-shaped, without any particular asymmetry, and is gently concave. Its ulnar edge is slightly sharper than its radial one. Two volar tubercles (radial and ulnar), separated by a notch, extend proximally beyond the Mc II facet. The shaft of the duplex is deepest in those specimens where fusion has proceeded most completely; in some specimens the junction of the original two bones has become obscured. Distally the duplex is expanded in the dorsal to volar direction by the curved facet for the ungual phalanx. This facet is shaped like a pulley, with a broad, deep groove between the two flanges, and curves from the dorsal edge of the distal end onto the volar surface of the duplex. Dorsally the groove comes to an end before the disappearance of its lateral flanges so that a stop for dorsal movement of the ungual phalanx is developed. On the volar side, the flanges of the articular facet curve apart and become sharper before they disappear.

When a number of duplexes from digit II of the manus are available, as in the Cook Collection ($N = 9$) and other collections from the Agate Quarries in the American Museum of Natural History, it becomes clear that two size groups are present. The smaller duplexes (Figs. 20C, D) are slightly less asymmetrical than the larger ones (Figs. 20A, B), and their proximal facet is not quite so flattened at its radial edge. The possibility that such smaller duplexes might belong to a digit other than digit II of the manus must be considered, especially in view of the occasional fusion of phalanges belonging to digit II of the pes. However, the difference in size in this case seems to be due to sex dimorphism, not to phalangeal fusion in additional digits. The mean length of the smaller manus duplexes in the Cook Collection (four specimens) is about 80% of that of the larger duplexes (six specimens). This ratio corresponds closely to the male/female size ratio calculated from the mean sizes of large and small radii and tibiae given by Coombs (1975). Rare duplexes, which do belong to digit II of the pes (see below), are only about two-thirds the size of the large ma-

nus duplexes and correspond closely to the combined lengths of unfused phalanges of digit II of the pes. Small or intermediate sized duplexes in schizotheriine species other than *M. elatus* must be evaluated carefully to determine whether they belong to the manus or the pes.

Digits III and IV of manus.—In *M. elatus* much of the great expansion of digit II of the manus is the result of expansion of the ungual phalanx and the part of the duplex representing the medial phalanx. The proximal phalanges of digits III and IV of the manus are not much smaller than the proximal part of the duplex. Because digit III and digit IV proximal phalanges are about the same size, it is difficult to assign each to the correct digit even though they differ from each other in morphology. One kind of proximal phalanx 1) is more symmetrical than the other sort, narrowing rapidly in the distal direction, 2) has metacarpal facets on its dorsal surface but with more proximal orientation than on the duplex, 3) has flattened articular areas on the dorsal surface just distal and adjacent to the metapodial facet (presumably for stops against hyperextension), 4) has some development of variable volar intermediate tubercles on the shaft, increasing the depth of the bone, and 5) has a slightly asymmetrical distal facet (a shallow, curved pulley).

A phalanx of YPM 24,632 (not mentioned by Marsh, 1877, but figured by Holland and Peterson, 1914:224) is among the second sort of proximal phalanx. Features include 1) transversely expanded metacarpal facet, 2) some lateral torsion of the shaft (more than in previous sort), 3) pronounced flattened area on dorsal surface just distal to the metacarpal facet and particularly noticeable on the ulnar (?) side, and 5) distal facet asymmetrical (one side of pulley longer and less curved).

Digit II of pes (Figs. 19C–F).—On a single individual the proximal phalanges of the pes are slightly smaller than those of the manus and are not so strongly expanded at their proximal ends. Digit II of the pes is represented by a comparatively large number of specimens from the Agate Quarries and Morava Ranch Quarry. In all of the specimens the bone is flattened in the dorsal to volar direction compared to most other proximal phalanges, and the articular facet for Mt II has a strongly dorsal orientation (a similarity to the facet for Mc II on the duplex of the manus). The Mt II facet extends onto the proximovolar tubercles, between which there is a pronounced notch. This notch is generally characteristic of the phalanx in its sharp indentation

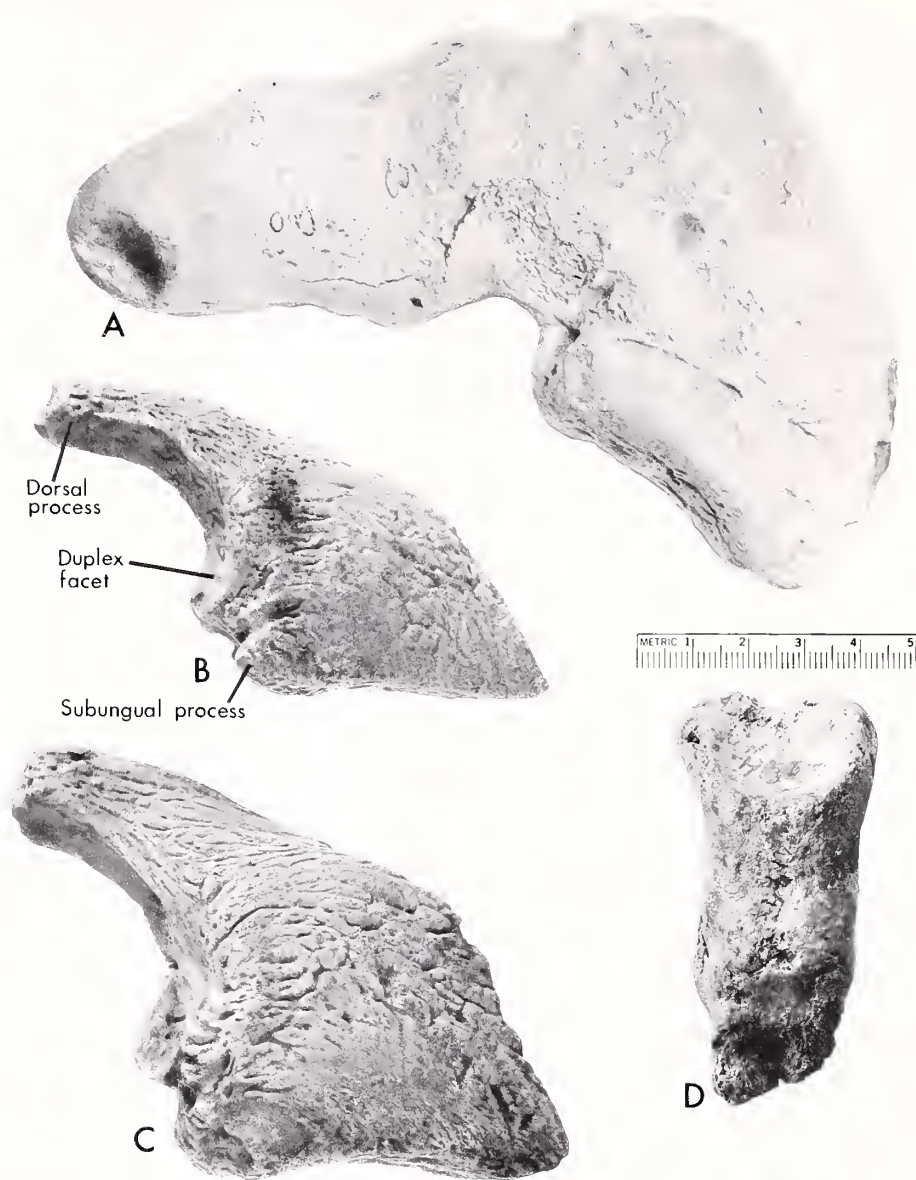


Fig. 21.—A) Unusual, completely fused proximal, medial, and ungual phalanges of digit II of the manus belonging to UCMP 14,377, *M. elatus*. B) Radial view of a left ungual phalanx of digit II of the manus of a presumed female of *M. elatus*, AMNH 14,425. C) Ulnar view of a right ungual phalanx of digit II of the manus of a presumed male of *M. elatus*, AMNH 14,427. All from the Agate Spring Quarries, Sioux Co., Nebraska. D) Dorsal view of fused proximal and medial phalanges of digit II of the pes of YPM 12,194, type of "*M. senex*," from Dayville, Oregon.

and small width. A distal facet for the medial phalanx, grooved but with an irregular surface, curves at the distovolar angle of the phalanx. The articulation between proximal and medial phalanges is so close that there could have been little or no movement between them (Figs. 19E, F). Holland and Peterson (1914:375–376) noted the occasional presence among the Carnegie material of fused proximal

and medial phalanges of digit II of the pes. Their observation is borne out by the presence among the Morava Ranch material (F:AM 54444, Figs. 19C, D) of another such example. A duplex for digit II of the pes is best distinguished from that of digit II of the manus by its smaller size and by its articular surface for the ungual phalanx being less deeply grooved and with less strongly flared volar edges.

Such fusion in the pes was quite uncommon in *M. elatus*, probably occurring in no more than one out of ten individuals.

Digits III and IV of pes.—Proximal phalanges of these digits are not easily distinguishable from one another. Both are longer and thicker than unfused proximal phalanges of digit II of the pes. One group of these phalanges (? of digit III) is slightly shorter and more expanded proximally than is the other group. In all of the specimens the articular surface for the metatarsal has more proximal orientation than is on the proximal phalanx of digit II. This difference is consistent with comparisons of digits III and IV of the manus against digit II, except that in the phalanges of the pes flat stopping surfaces at the distal edge of the metatarsal facet are small or absent. This difference probably corresponds to the smaller development on the metatarsals of the tubercles against which the flattened areas of the phalanges may rest during hyperextension. Both phalanges are more symmetrical than their counterparts in the manus.

Medial Phalanges

Unfused medial phalanges of manus and pes are not easily distinguished in this species. All have a curved concave proximal facet (for the proximal phalanx), divided into two halves by a ridge, and a pulley-like, curved distal facet for the ungual phalanx. Medial phalanges of digits III and/or IV of the manus are more likely than others to have asymmetrical development of the proximal facet. The medial phalanx of digit II of the pes, even where it has not fused to the proximal phalanx, has a right angle bend in its proximal facet which would prevent any movement of the two phalanges against one another.

Ungual Phalanges (Figs. 21B, C)

Except for the large ungual of digit II of the manus, it is practically impossible to refer ungual phalanges to a given digit, except that in a given individual, unguals of the manus are usually larger than those of the pes.

The large ungual phalanx of digit II of the manus is taller and more transversely compressed than other unguals of this species, and there is a thick, tall dorsal process onto which the duplex facet extends. A large, rugose subungual process prevents the duplex facet from reaching the volar surface of the bone. Although the duplex facet covers a large arc at the proximal end of the ungual phalanx, it

does not follow an evenly rounded curve but has a sharp angle between its proximal oriented and volar oriented parts; this angle corresponds to one on the distal facet of the duplex and effectively prevents most movement between the two bones. Dorsally the claws are quite sharp, and there is either equal fission between the dorsal and volar edges of the claws or greater fission dorsally.

An intermediate sized ungual, not so tall nor so strongly compressed transversely as the larger one, belongs to digit III or IV of the manus and has both a large dorsal process and subungual process. As in the larger phalanx, the claws are sharp and cloven equally above and below. The other ungual of the manus compares closely with the unguals of the pes.

Of the three small pes unguals one has a larger dorsal process than the others. Generally the pes unguals are relatively broad transversely, and the two claw sides are separated by a small space. The two sides may be slightly asymmetrical and are usually cloven more deeply above than below. The subungual process is much reduced.

Sesamoids

A number of sesamoids are known in *M. elatus*. These articulate with the distovolar surfaces of metacarpals and metatarsals, but it is difficult to determine, which sesamoids go with which digits.

Moropus distans Marsh

Moropus distans Marsh, 1877:249.

Moropus distans: Peterson, 1907b:734; Holland and Peterson, 1914:221; von Koenigswald, 1932:22; Colbert, 1935:13; Belyaeva, 1954:49 (locality incorrectly cited as Nebraska by von Koenigswald, Colbert, and Belyaeva).

LECTOTYPE

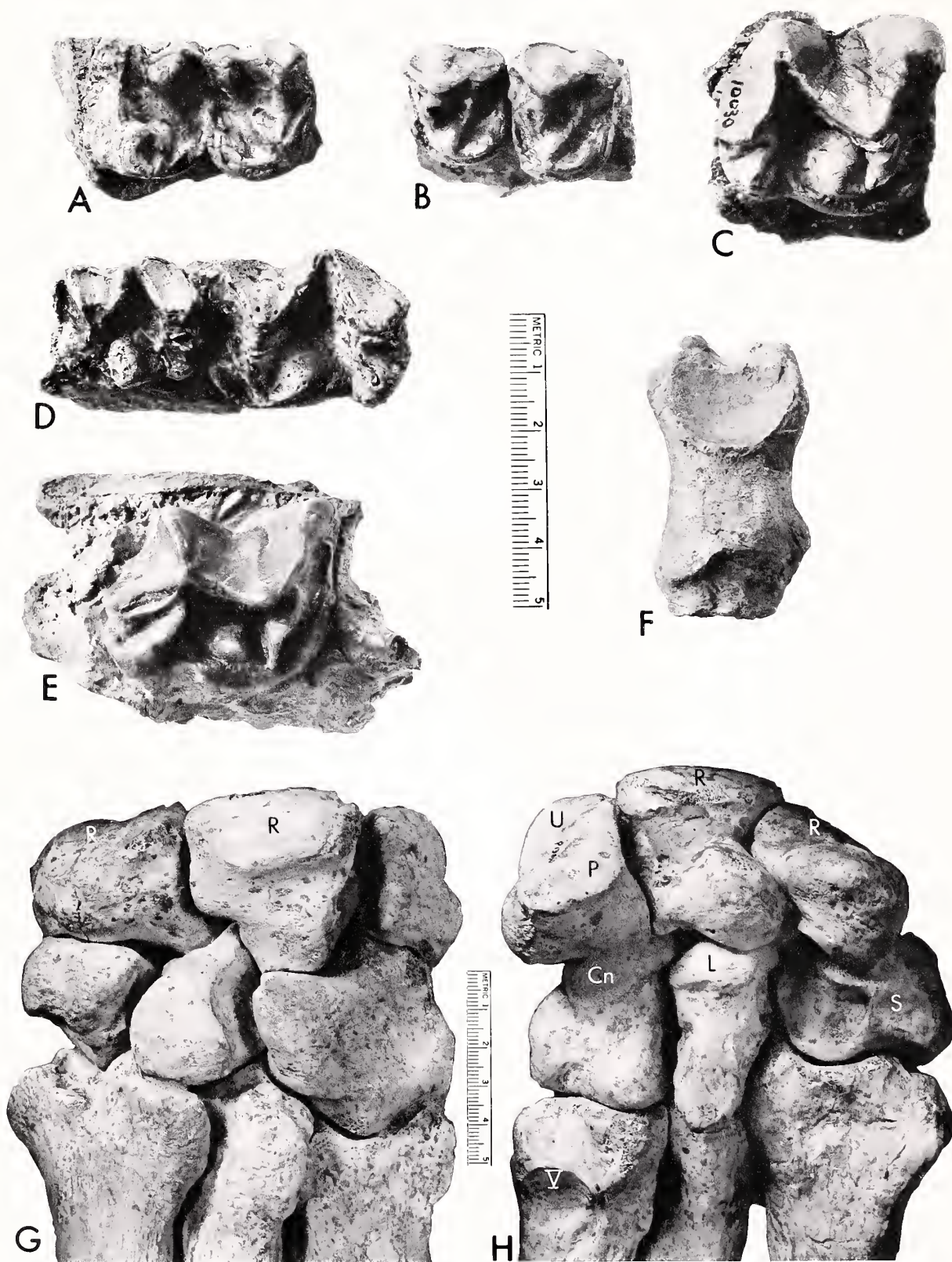
YPM 12,193a, coossified proximal and medial phalanges (duplex) of digit II of pes from the "Bridge Creek beds" in the John Day Basin, Oregon, ?Arikareean (Fig. 22F).

PARALECTOTYPE

Medial phalanx of YPM 24,627 mentioned by Marsh (1877).

HYPODIGM

Cuboid of YPM 24,628, first mentioned and figured by Holland and Peterson (1914:220; see Figs. 16C, F); distal end of Mc II of YPM 24,628. Paralectotype and hypodigm were collected with the lec-



totype and were originally given the same catalogue number; however, they are probably not the same individual and are renumbered in this paper.

DIAGNOSIS

A small chalicotheres, smaller than any known specimen of *M. elatus*; cuboid having more proximal extension of navicular facet than in *M. elatus*; duplex of digit II of pes flatter in dorsal to volar direction than rare pes duplexes of *M. elatus*, fusion to form this duplex possibly more common than in *M. elatus*.

DISCUSSION

Although *Moropus distans* is not so well known as *M. elatus*, Holland and Peterson (1914:217) established it as the type species of *Moropus* because Marsh (1877) had mentioned it first. Additional material must be obtained before an estimate of the size range in this species can be made. Small average size may be a primitive feature in the genus *Moropus* (see also *Moropus* sp. from St.-Gérandle-Puy, Coombs, 1974). The distribution of *M. distans* cannot be evaluated without fuller knowledge of other small, early North American chalicotheres, for the species is presently known only from Oregon.

Attention is directed to *Moropus oregonensis* (Leidy, 1873) from the same region as *M. distans*. Both species were described before it became known that the teeth and footbones of chalicotheres actually belong to the same kind of animal (Filhol, 1891). *M. distans* may be synonymous with *M. oregonensis*, which includes only teeth, but conspecificity cannot be established. If evidence of synonymy should become available, *M. oregonensis* (discussed below) would become the type species of *Moropus*.

Marsh (1877:250) also named *Moropus senex* for a duplex, YPM 12,194 (Fig. 21D), from near Dayville, Oregon. This phalanx, which belongs to digit II of the pes, is described below but has no specific diagnostic features. *Moropus senex* is therefore considered to be a *nomen dubium*. The type spec-

imen resembles rare pes duplexes of *M. elatus* but is considered for the present to represent *Moropus* indet.

DESCRIPTION AND COMMENTS

YPM 12,193a, the small duplex here designated as the lectotype of *Moropus distans* (Fig. 22F), appears to belong to digit II of the pes but is slightly flatter, especially in the metapodial facet, than duplexes of the same digit in *M. elatus* and "*M. senex*." Its distal end is not known, and thus definite identification as a duplex of the pes cannot be made, despite its small size. In addition to its unusually small size compared to other *Moropus* specimens, this duplex may be significant in the mere presence of fusion of proximal and medial phalanges in a pes digit, for such fusion is rare in *M. elatus* (no more than 10% of known specimens). Although it is hazardous to generalize on the basis of limited material, the presence of such a duplex among the very few specimens of *M. distans* may suggest that development of a pes duplex was common in this species. Formation of a duplex for pes digit II is apparently universal in certain *Moropus* species, for example *M. merriami*.

Fusion of phalanges to form a duplex of pes digit II is also of interest in the single specimen of "*M. senex*," YPM 12,194 (Fig. 21D). This specimen clearly belongs to digit II of the pes by virtue of its shallow distal facet without flared lateral edges. It is thus not a manus duplex, unless an unusual one, of a small sized *Moropus* species. Morphological resemblances to an *M. elatus* duplex of pes digit II from Morava Ranch Quarry (F:AM 54,444, Figs. 19C, D), including a size similarity, make tempting a synonymy of "*M. senex*" with *M. elatus*. YPM 12,194 does not seem to belong to *M. distans*, but the rarity of phalangeal fusion in the pes of *M. elatus* and our lack of knowledge of postcranials of *M. oregonensis* make any taxonomic alignment of "*M. senex*" premature.

YPM 24,627, the medial phalanx paralectotype of *M. distans*, presents no features of special taxonomic interest, except for small size, nor does the

Fig. 22.—A) Holotype of *M. oregonensis*, YPM 10,030, a right maxillary fragment with P⁴ and partial M¹. B–E) Hypodigm of *M. oregonensis*: left P³–P⁴ (B) and right M³ (C) of YPM 10,030a; left M¹–M² (D) of YPM 10,030b; and right M³ (E) of AMNH 7259. F) Lectotype of *M. distans*, YPM 12,193a, coossified proximal and medial phalanges of digit II of the pes. A–D and F are from the "Bridge Creek Beds" in the John Day Basin, Oregon; E is from "near Antelope Springs," Oregon. G and H) Dorsal (G) and volar (H) views of a left carpus of *M. hollandi*, FMNH P13000 (minus pisiform), from near Jay Em, Goshen Co., Wyoming. Bones correspond to those of right carpus of *M. elatus* labeled in Fig. 9; facet abbreviations as given in Fig. 10.

Mc II distal end of YPM 24,628. Both specimens generally resemble their counterparts in *M. elatus* except that the two sesamoid facets on the *M. distans* Mc II are slightly less unequal in size than they are in *M. elatus*.

The cuboid of YPM 24,628 is small, with a maximum dorsal to volar thickness of 47 mm, compared with 75 mm for AMNH 14,378 (a medium-sized cuboid of *M. elatus*). Morphologically, the specimen is close to cuboids of *M. elatus*, *M. hollandi*, and *M. merriami*, but the tibiovolar rugose process is proportionately somewhat smaller than in other *Moropus* specimens (Figs. 16C, F). Unfortunately the volar part of the tibial side of the bone is damaged, so that the extent of navicular and ectocuneiform facets are not completely clear. Nevertheless, the navicular facet appears to extend proximally to reach the proximal edge of the tibial side and thus adjoins the facet for the calcaneum (Fig. 16C). Such proximal extension of the navicular facet is seen in *M. merriami* (UCMP 78,727) but not in *M. elatus* or *M. hollandi*. The ectocuneiform facet on the *M. distans* cuboid, though broken at its volar edge, is apparently single rather than double; *M. elatus* has variably a single or double facet, but more typically a double one.

Moropus oregonensis (Leidy)

Lophiodon oregonensis Leidy, 1873, pl. 2, fig. 1 (also described without name pp. 219–220).

Lophiodon oregonensis: Sinclair, 1901:702.

Moropus oregonensis: Holland and Peterson, 1914:219; Colbert, 1935:13; Belyaeva 1954:49.

HOLOTYPE

YPM 10,030, right maxillary fragment with worn P⁴ and partial M¹ from Bridge Creek area, John Day Basin, Oregon (specimen label states "upper John Day beds"); ?Arikareean; see Fig. 22A.

HYPODIGM

Left P³-P⁴ and right M³ of YPM 10,030a, which may be part of the same individual as the type but were not figured by Leidy (Figs. 22B, C); YPM 10,030b, left M¹-M² collected at the same locality as type (Fig. 22D); AMNH 7259, M³ (Fig. 22E) from "near Antelope Springs, Oregon."

DIAGNOSIS

Species known only from dental remains, smaller than the smallest known representatives of *M. elatus*; metaloph on unworn upper molars (especially

M³) with labial origin very close to mesostyle, even closer than in *M. elatus*; upper molars not strongly elongated; P³ and P⁴ without strong anterolingual or posterolingual cingula and with wear along transverse loph proceeding to protocone before lophs are completely worn away (especially along metaloph).

DISCUSSION

Like *Moropus distans*, *Moropus oregonensis* shows a number of similarities to *Moropus merriami* and some of its undescribed Hemingfordian relatives, possibly more resemblance than to *Moropus elatus*. Although of small size, the known teeth of *M. oregonensis* are slightly larger than might be expected to belong to the same individuals as the small postcranials of *M. distans*. Nevertheless these two species may be synonymous, for the possibility of sexually dimorphic size differences must be considered. The labial origin of the metaloph so close to the mesostyle on unworn M³ is a character shared with *Schizotherium* (see *S. priscum* in Coombs, 1976); it is apparently primitive within the genus *Moropus* and is lessened in more advanced species.

DESCRIPTION AND COMMENTS

M³ (Figs. 22C, E).—The two available specimens, YPM 10,030a and AMNH 7259, are of similar size. At a glance they appear to have quite different morphology, but most of the points of variance are easily explained by wear, for AMNH 7259 had only recently erupted. In the unworn tooth the origin of the metaloph is very close to the mesostyle, whereas in the worn tooth the origin has moved posterolingually. All parts of the metaloph are of approximately equal height, but there is a slightly separated summit, representing the hypocone, at the lingual end of the metaloph. The anterior part of the tooth, including the relatively large protocone and complete protoloph, is little worn even on the more worn specimen, YPM 10,030a. In neither specimen does a branch of the anterolingual cingulum join the protoloph to ascend to the tip of the protocone. In YPM 10,030a, the anterolingual cingulum remains separate, ridge-like and uniform as it skirts the protocone lingually; posteriorly it enters the central valley as a weak ridge or fold but does not close off the lingual opening of the central valley. In AMNH 7259 the cingulum is less uniform and approaches the wall of the protocone more closely but does not fuse with it. The postfossette

is partly closed off by the posterior cingulum, and a labial rib is present opposite the paracone. On AMNH 7259 a very small crista (see Butler, 1965:178, for definition) is present. Principal differences from *M. elatus* include the smaller degree of wear on the protoloph and the morphology of the anterolingual cingulum. The origin of the metaloph is closer to the mesostyle in an unworn specimen than in any other known *Moropus* species, even *M. elatus*.

M² and M¹ (Fig. 22D).—In addition to its smaller size, *M¹* is more quadrate (less elongated compared to width) than *M²*. Both teeth closely resemble *M³*, but on *M²* a branch of the anterolingual cingulum appears to join the protoloph (but weakly), in contrast to *M³*. The parastyle and mesostyle, particularly on *M²*, are slightly weaker than they are in *M. elatus*. Posterior to the protocone the lingual cingulum is only weakly visible.

P³ and P⁴ (Figs. 22A, B).—Known upper premolars are somewhat worn. They show many similarities to specimens of *M. elatus*, but in their pattern of wear come closer to some of the small Hemingfordian relatives of *M. merriami*. It is clear, despite wear, that the two transverse lophs were complete and that a protoconule was present. Wear reaches the protocone earlier in the life of each tooth than it does in *P³* and *P⁴* of *M. elatus*, for in these specimens the protocone has been worn nearly flat and lies quite below the level of the protoloph at the same time that the protoloph is still completely or at least partially visible. Apparently wear proceeds from the ectoloph along the metaloph to the tip of the protocone fairly early during the life of the animal, whereas wear along the protoloph is much slower. Wear on the anterior part of the ectoloph slightly reduces the parastyle in comparison to that often seen in even more worn specimens of *M. elatus*. Anterolingual and posterolingual cingula are not at all expanded but form a uniform ridge skirting the protocone, fusing with it at only one point.

***Moropus hollandi* Peterson**

Moropus elatus: Peterson, 1907a:60.

Moropus hollandi: Peterson, 1913:673.

Moropus hollandi: Holland and Peterson, 1914:232.

Moropus elatus: Matthew, 1929:520.

Moropus hollandi: von Koenigswald, 1932:22; Colbert, 1935:13; Belyaeva, 1954:49.

HOLOTYPE

CM 1424, a partial skeleton of a medium-sized individual, including radius-ulna, scaphoid, trape-

zoid, magnum, unciform, Mc II-V, femur, two tibiae, two astragali, two calcanea, duplex of digit II of manus, proximal phalanx, and medial phalanx, from Peterson's (1907a) Upper Harrison beds near Nebraska-Wyoming state line along Niobrara River. Early Hemingfordian. Many of the elements of the holotype of *M. hollandi* were figured by Holland and Peterson (1914) and, except for the scaphoid and trapezoid (Figs. 26E-H), are not repeated in the present paper.

HYPODIGM

F:AM 54902a-1, two scaphoids (Fig. 26C), two lunates (Fig. 26D), distal end of radius, distal end of radius-ulna, cervical vertebra VII, two proximal phalanges, astragalus (Fig. 23C), sesamoid, proximal end of ulna, and cuboid, from Upper Harrison equivalent beds (Skinner, 1968) 7 mi south of Chugwater, Wyoming; FMNH P13000, an atlas (Fig. 6B), pelvis, almost complete left manus (Figs. 22G, H, 24, 25, 26A, B), duplex and ungual phalanx of digit II of manus (Figs. 28D-F), and navicular, cuboid, and Mt III of left pes (Figs. 16A, D, G, 27B, D-F) from "Jay Em Creek, 2 mi east of ranch, Lusk, Wyoming;" and FMNH P12094, a skull (Figs. 23A, B) from the "east wall of Jay Em Creek, a tributary of Rawhide Creek, near Lusk, Wyoming." The Field Museum specimens, collected by Riggs near Jay Em, probably also come from Upper Harrison equivalent beds. All the material referred to F:AM 54,902 is larger than the holotype, and some of it probably belongs to a single individual.

ADDITIONAL MATERIAL

F:AM 54,903, a Mt III and Mt IV from Upper Harrison equivalent beds (Skinner, 1968) near Jay Em, Wyoming, is here referred to *Moropus* cf. *M. hollandi*. Its uncertain reference is because of differences, whose significance is unclear, between its Mt III (Figs. 27C, 28A-C) and that of FMNH P13000. The latter specimen is more definitely referable to *M. hollandi* by virtue of its known manus morphology.

DIAGNOSIS

Moropus species resembling *M. elatus* in most respects, including size, dental morphology, and absence of proximal extension of navicular facet on the cuboid. Differs from *M. elatus* in the generally shorter proportions of Mt III relative to minimum shaft width (Table 6) and from all known *Moropus* species in the absence or strong reduction of a tra-

pezium in the manus. Trapezium facets absent on scaphoid, Mc II, and probably on trapezoid. Lunate, cuneiform, and trapezoid commonly compressed in the dorsal to volar direction relative to their width.

DISCUSSION

The Frick and Field Museum specimens cited in the hypodigm are of great importance in affirming *M. hollandi* as a separate species. Three additional scaphoids, one trapezoid, and one Mc II, all of which closely resemble the holotype, and new metatarsal specimens reinforce the idea that the differences of the holotype of *M. hollandi* from *M. elatus* are not mere individual peculiarities. Absence of a trapezium, along with the dorsal to volar compression of several carpals, suggests a degree of superflexion of the manus unusual within *Moropus*.

The large number of similarities between *M. hollandi* and *M. elatus* emphasize the close affinities between these two species. At the same time they create difficulties in identifying specimens, especially in those many cases where diagnostic elements of *M. hollandi* are not included. Because of difficulties in identification, it is still unclear whether the two species are separated by a temporal boundary or whether their occurrences reflect ecological differences in the assemblages in which they are represented. Additional specimens may someday show a morphological continuity in the evolution of *M. hollandi* from a population of *M. elatus*. Certainly some aspects of *M. elatus* morphology, when taken at one end of their range of variation (for example, shorter proportions of some metatarsals) approach conditions seen in *M. hollandi*. On the other hand, no *M. elatus* specimen shows the scaphoid, trapezoid, or Mc II characteristics considered diagnostic of *M. hollandi*.

Absence of a trapezium occurs in *Moropus*, so far as is known, only in *M. hollandi*. It is paralleled, however, in *Ancylotherium* (*Ancylotherium*) *pentelicum*, where there is an even greater degree of mobility of the scaphoid on the trapezoid. There the scaphoid contacts Mc II during extreme flexion as was reported by Schaub (1943; although Schaub concluded, probably erroneously, that the trapezium in *Ancylotherium* was fused with Mc II). *Schizotherium turgaicum* and *Borissiakia betpakdalensis* apparently have also independently lost the trapezium (see Borissiak, 1946; Belyaeva, 1954).

Slight proportionate shortening of the metatarsals

of *M. hollandi* compared to *M. elatus* is consistent with the gradual shortening over time of metatarsals among a number of schizotheriine species (see Coombs, 1974). The Mt IV proportions of F:AM 54,903 (*Moropus* cf. *M. hollandi*) most closely approach those of the small Mt IV of *Moropus* sp. from Aquitanian deposits of St.-Gérard-le-Puy, Allier, France (Table 6).

Present evidence suggests that *M. hollandi* had a size range rather similar to that of *M. elatus*. The two best preserved individuals (the holotype and FMNH P13000) are of modest size, however, but material in F:AM 54,902 suggests that larger individuals were also included in the species. The holotype and FMNH P13000 probably represent females, and the morphology of their duplex phalanges of the manus also supports this conclusion (see discussion of *M. elatus* duplexes).

DESCRIPTION AND COMMENTS

Skull and Upper Dentition (FMNH P12094, Figs. 23A, B)

The single skull with upper teeth known for *M. hollandi* falls within the range of morphology of *M. elatus* and shows no special differentiating features. There is no sign of doming or skull elaboration, and certain landmarks, like the internal nares and infraorbital foramen, are in the same position as they are in *M. elatus*. The upper teeth also cannot be differentiated from those of *M. elatus*, although the length of the toothrow (P^2 - M^3) falls near the lower end of the *M. elatus* size range and the premolar row may be proportionately shorter. The teeth in this specimen are very little worn, so that the protoconule and protoloph on M^3 are still complete. The labial origin of the metaloph on M^3 is still quite close to (less than 10 mm from) the lingual base of the mesostyle. The base of the protocone is not folded in the central valley. Premolars of FMNH P12094 are most similar to those specimens of *M. elatus* in which the protoloph of P^2 is not strongly developed and the lingual cingula of P^3 and P^4 are relatively small. On P^3 and P^4 the protoloph is taller than the metaloph, which is more worn. Despite the progressing wear on protoloph and especially metaloph, the protocone is still completely unworn, a similarity in wear pattern to *M. elatus* as compared to *M. oregonensis*.

Vertebrae and Pelvis

The atlas and pelvis (FMNH P13000) cannot be easily differentiated from specimens of *M. elatus*.

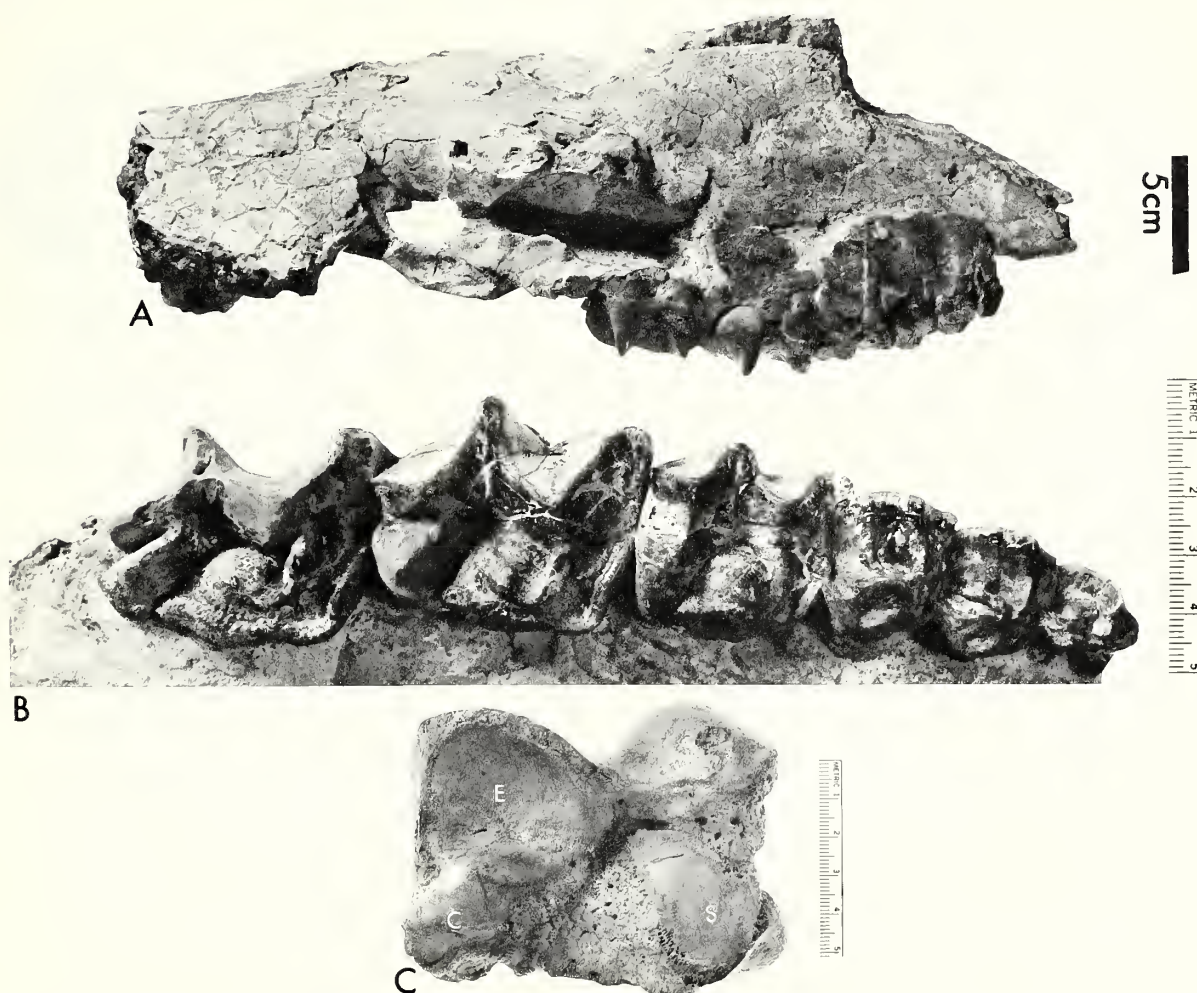


Fig. 23.—Lateral view of skull (A) and occlusal view of right P²-M³ (B) of *M. hollandi*, FMNH P12,094, from near Jay Em, Goshen Co., Wyoming. Volar view of astragalus (C) of F:AM 54,902g, referred to *M. hollandi*, from 7 mi south of Chugwater, Wyoming. For facet abbreviations on astragalus see Fig. 14.

However, the proportions of the atlas are slightly different (see Fig. 6), for the anterior to posterior length of the ventral arch is small relative to the transverse width of the articular surfaces for the occipital condyles. F:AM 54,902e, a cervical vertebra VII, corresponds generally with specimens of *M. elatus* but is also rather broad, particularly anteriorly.

Forelimb

CM 1424, the holotype of *M. hollandi*, includes much of one forefoot; additional forelimb material belonging to F:AM 54,902 and FMNH P13000 makes the forefoot the best known part of the skeleton of *M. hollandi*. The fused radius-ulna of CM 1424 does not differ from specimens of *M. elatus* in

any important way but is strongly fused into a single unit for more of its length than are most *M. elatus* specimens. There is a slight difference between F:AM 54,902c and F:AM 54,902d, both of which include the distal ends of radii, in that the former has a more strongly compressed and dorsal to volar concave distal facet for the lunate. The less compressed condition (F:AM 54,902d) is more similar to that in *M. elatus*, but the compressed condition corresponds more closely to the morphology of the lunate of F:AM 54902b (Fig. 26).

The carpus provides the principal characters by which *M. hollandi* is distinguished from *M. elatus*. The scaphoid differs from that of *M. elatus* in the apparent lack (or at least very strong reduction) of a trapezium facet, so prominent on the radiovolar

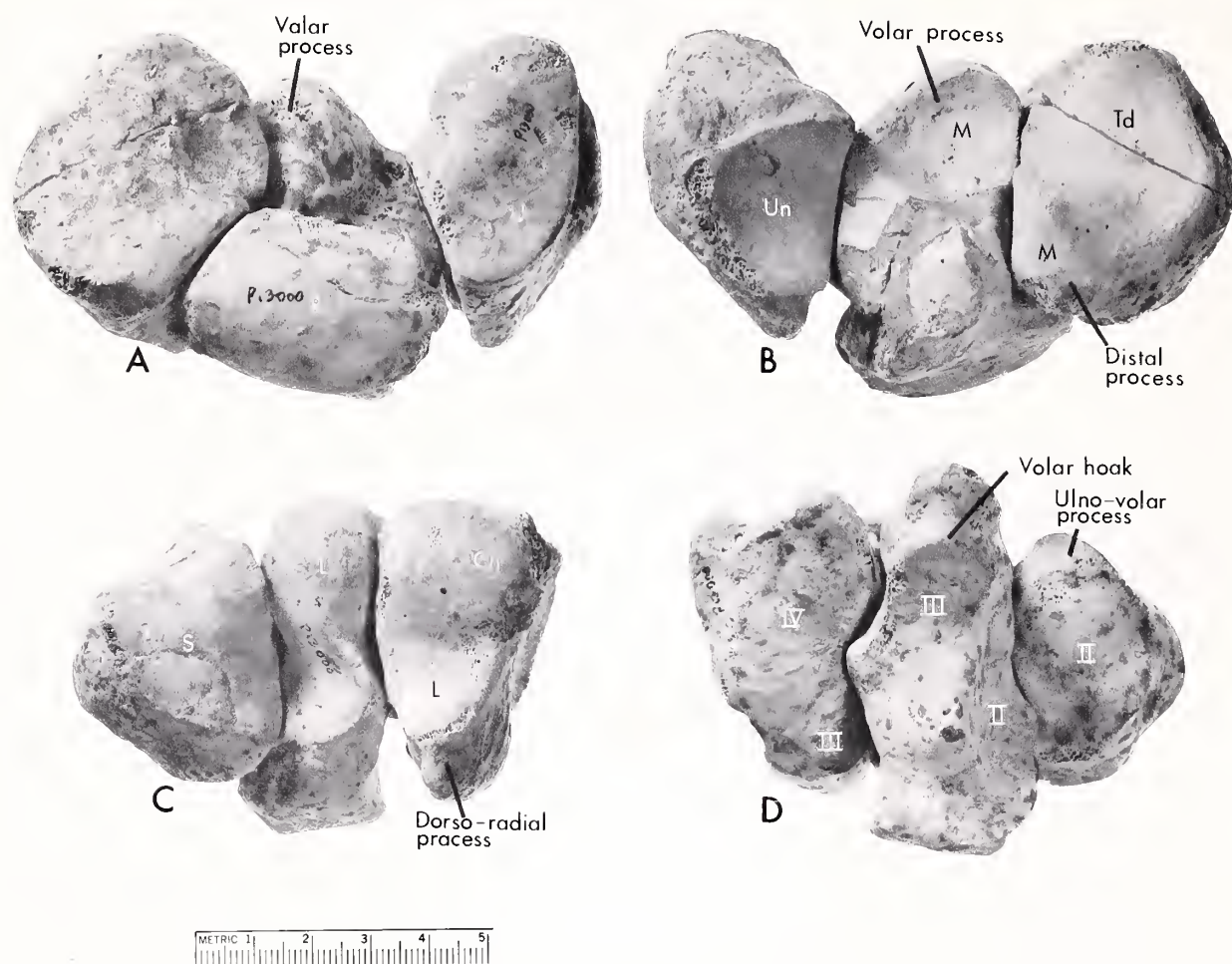


Fig. 24.—Proximal (A, C, radial edge at left) and distal (B, D, radial edge at right) views of left scaphoid, lunate, and triquetrum (A, B) and left trapezoid, magnum, and unciform (C, D) of *M. hollandi*, FMNH P13000, from near Jay Em, Goshen Co., Wyoming. Facet abbreviations as in Fig. 10.

surface of the scaphoid in other *Moropus* species. In *M. hollandi*, the same area is occupied by a ridge separating the rough radiovolar surface from the smooth saddle-shaped trapezoid facet distal to it (Figs. 22H, 26A, C, E). The trapezoid facet (Fig. 24B) is very similar to its counterpart in *M. elatus*, as is the proximal lunate facet (Figs. 26B, F). The distal lunate facet is also similar but does not extend so far in the proximal and volar directions; however, it does reach the edge of the trapezoid facet in its most proximal part. As in *M. elatus*, the distal process is squared with a relatively flat magnum facet on its distal surface, bordered by trapezoid and distal lunate facets (Fig. 24B).

Two lunate specimens are slightly compressed in the dorsal to volar direction, with proximal and dis-

tal scaphoid facets curtailed at their volar edges (Fig. 25A). In F:AM 54.902b (Fig. 26D) the volar process is also rather short, and the facet for the radius is very strongly convex in a dorsal to volar direction and abbreviated at its volar edge. A third, larger, specimen (F:AM 54.902k) has a large volar process and does not seem to be compressed.

The single cuneiform specimen, like the lunate of the same individual (FMNH P13000), shows a tendency toward compression in a dorsal to volar direction. Such abbreviation on the cuneiform is mostly in the lunate (Fig. 25C) and unciform (Fig. 24B) facets; the unciform facet is more concave than in specimens of *M. elatus* and is set off by a volar ridge.

The unciform (two specimens) is basically similar

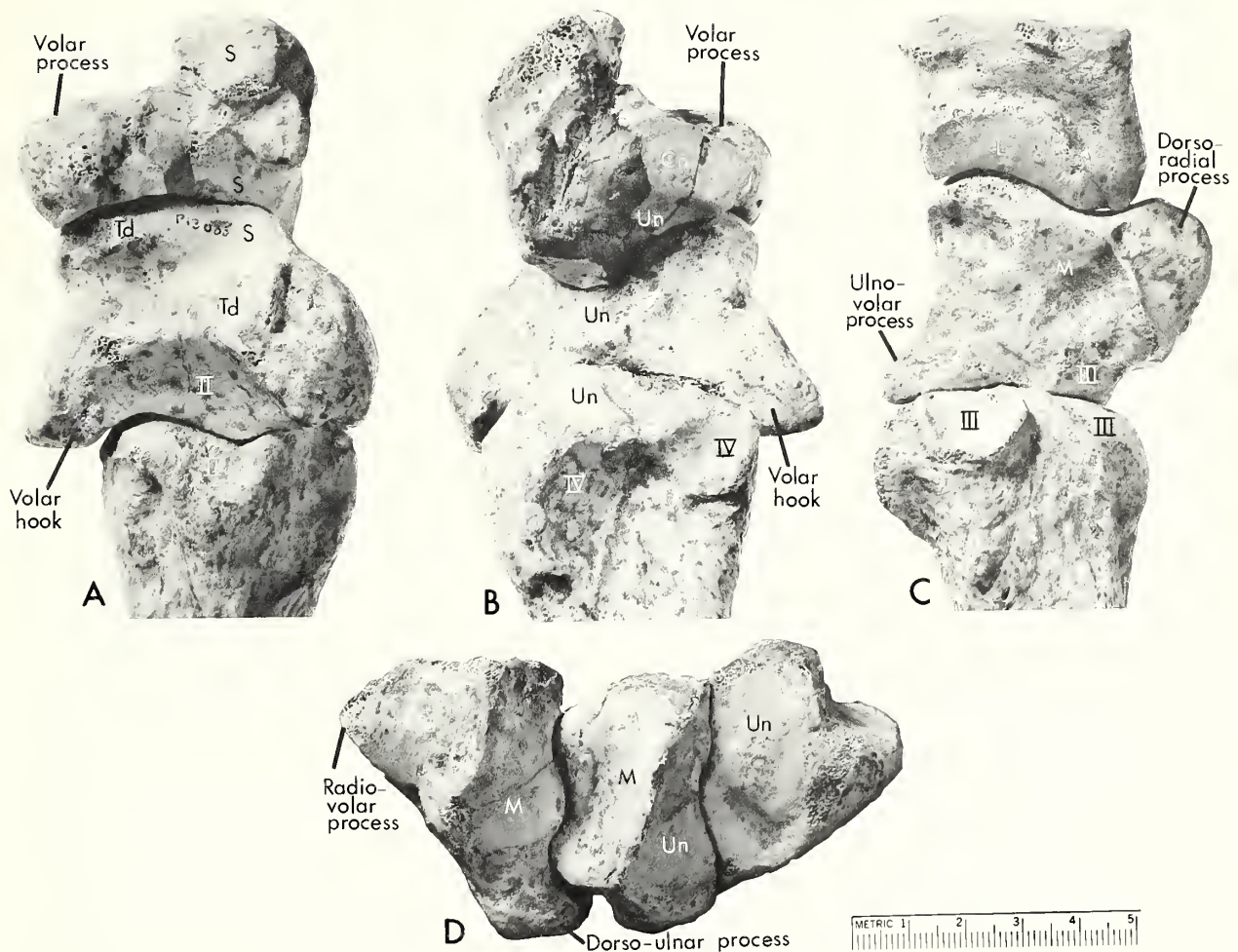


Fig. 25.—A) Radial view of left lunate, magnum, and Mc III (dorsal edge at right), B) ulnar view of left lunate, magnum, and Mc III (dorsal edge at left), C) radial view of left cuneiform, unciform, and Mc IV (dorsal edge at left), and D) proximal view of left Mc II, Mc III, and Mc IV (dorsal edge below, radial at left) of *M. hollandi*, FMNH P13000, from near Jay Em, Goshen Co., Wyoming. Facet abbreviations as in Fig. 10.

to that of *M. elatus*. On the radial surface (Fig. 25C), the platformed magnum facet extends farther distally, however, and is separated from the Mc III facet by a clearly defined ridge. Distinctness and slant of the magnum facet of these specimens resembles those in Morava Ranch Quarry specimens of *M. elatus* slightly more than those from Agate. At its proximal edge the magnum facet has a narrow proximal strip of facet passing in a volar direction from the main body of the facet and bordering the radial edge of the lunate facet for some distance; this addition to the magnum facet is present in some but not all *M. elatus* specimens and presumably allows tighter articulation between magnum and unciform. As in *M. elatus*, the boundary between Mc III and Mc IV facets is indistinct. Because of the

great distal extent of the magnum facet, that for Mc III is a bit smaller than the one in *M. elatus*; there appears to be another tiny area of contact with Mc III, only rarely present in *M. elatus*, on the radial side of the ulno-volar process.

The two known magnum specimens resemble material of *M. elatus* very closely, except that the more distal extension of the contact between magnum and unciform is reflected in a flat and rather inconspicuous distal continuation of the unciform facet on the magnum (Fig. 25D).

The trapezoid differs from that of *M. elatus* in several points, the most important being the absence of a trapezium facet. The scaphoid facet of CM 1424 (Fig. 26G), like that of *M. elatus*, curves onto the radiovolar surface of the trapezoid, but

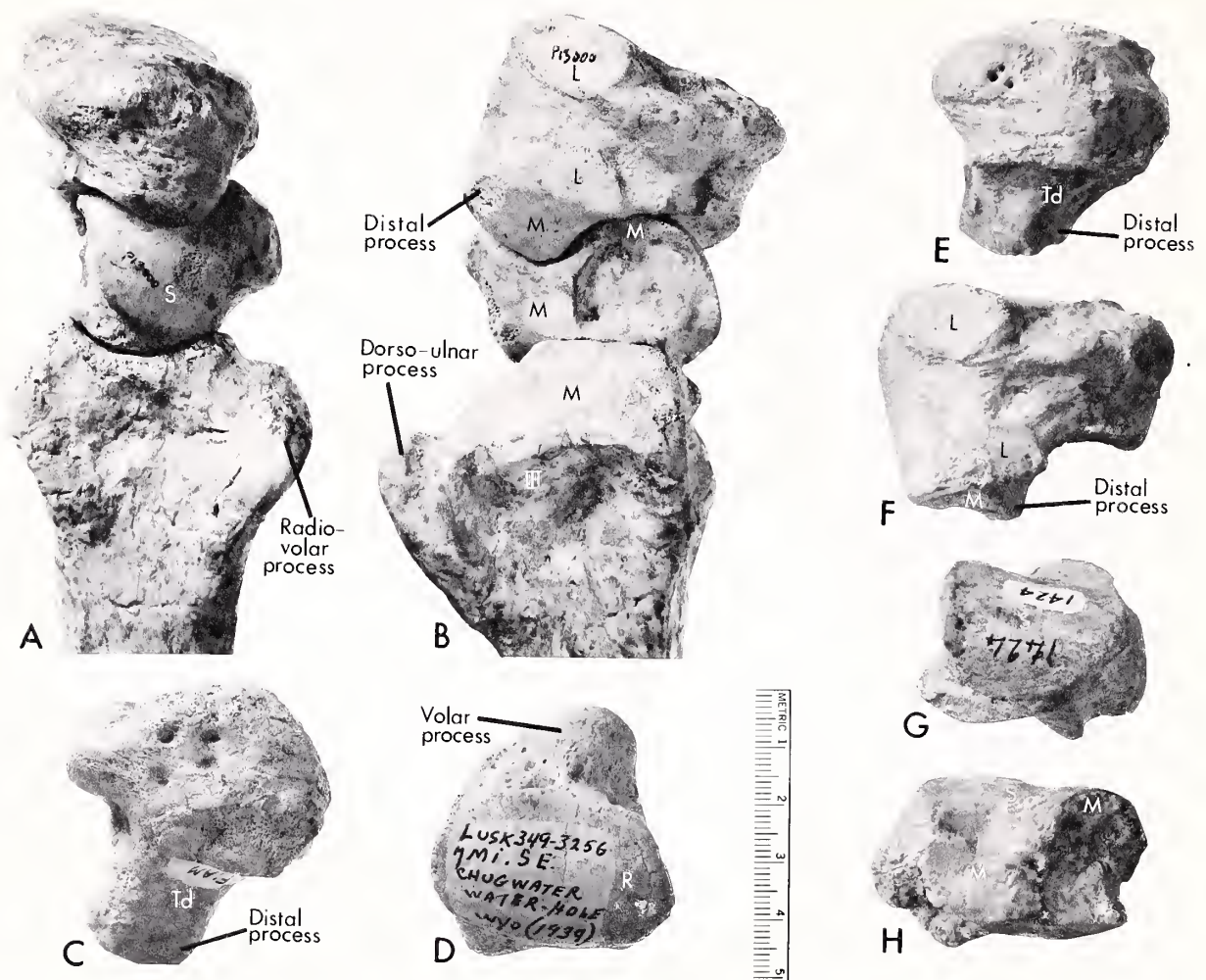


Fig. 26.—A) Radiovolar view of left scaphoid, trapezoid, and Mc II, and B) ulnar view (dorsal edge at left) of left scaphoid, trapezoid, and Mc II of *M. hollandi*, FMNH P13000, from near Jay Em, Goshen Co., Wyoming. C) Radiovolar view of left scaphoid of *M. hollandi*, F:AM 54.902a, and D) proximal view (volar edge below) of right lunate of *M. hollandi*, F:AM 54.902b, both from 7 mi south of Chugwater, Wyoming. E) Radiovolar, and F) ulnar views of left scaphoid, and G) radiovolar, and H) ulnar views of left trapezoid of holotype of *M. hollandi*, CM 1424, from near the Wyoming state line along the Niobrara River, Sioux Co., Nebraska. Facet abbreviations as in Fig. 10.

instead of merging with a facet for a trapezium, it passes distally for almost the height of the trapezoid. It does not, however, quite adjoin the Mc II facet at the distal end of the trapezoid but is shaped like a tongue with its volar and distal edges especially well defined. When the scaphoid is moved along the trapezoid, its concave distal surface follows the contour of this facet all the way to the distal edge of the trapezoid. This range of movement suggests that the entire radiovolar facet was indeed for the scaphoid. The scaphoid facet in FMNH P13000 (Fig. 26A), although resembling that in *M. elatus* in not being clearly abbreviated at its

distal edge, was probably also only for the scaphoid. Scaphoid and Mc II in this specimen show no trace of trapezium facets, and the scaphoid during extreme flexion of the carpus reaches close to the trapezoid's distal edge. It is probable, considering the absence of trapezium facets on scaphoid, trapezoid, and Mc II, that no trapezium was present in *M. hollandi*. This possibility was mentioned by Holland and Peterson (1914:233), but their evidence for it was not so strong, for they thought that a trapezium facet was present on the trapezoid. Trapezoids of *M. hollandi* also are more abbreviated at their volar edges than are those of *M. elatus*.

Mc II (two specimens) shows basic similarity in articular facets to Mc II of *M. elatus*, including the following: 1) the concave nature of the trapezoid facet, which is set off by well-defined ridges from all other facets (Fig. 25D); 2) the lack of strong proximal orientation of the volar part of the magnum facet and of any sharp ridge separating it from the trapezoid facet (Fig. 25D); 3) Mc III facet overhung for almost all of its extent by the magnum facet (Fig. 26B). These features are not shared by certain other North American schizotheriine species. The radiovolar angle of the proximal end of Mc II differs from all known *Moropus* species in the absence of a trapezium facet and the weakly developed radiovolar process (Fig. 25D). There is no difference from *M. elatus* in the shaft or distal end.

The proximal end of Mc III is narrower in relation to its depth than in other *Moropus* species, and this narrowness is reflected in the shape of the proximal facets. The proximal part of the Mc II facet is flatter than that in *M. elatus* and slants more dorsally (Fig. 25A); as in *M. elatus* it is continuous with the dorsal part of the Mc II facet. Magnum and unciform facets (Fig. 25D) are both narrower than, but otherwise similar to, the same facets in *M. elatus*. On the ulnar side of Mc III, weakly overhung by the unciform facet, are two Mc IV facets in the holotype, the dorsal facet larger and separated from the volar one by a depression of greater width than any seen on specimens of *M. elatus*. However, the joining of these two facets in FMNH P13000 (Fig. 25B) suggests that variability of the Mc IV facet(s) persisted in *M. hollandi*. Shaft and distal end of Mc IV are similar to those in *M. elatus*.

Mc IV is quite similar to its counterpart in *M. elatus*. There are two separate articular facets for Mc III (Fig. 25C); the dorsal facet differs in the holotype from that in *M. elatus* in being not much larger than the volar facet, in being concave, and in having an orientation far more radial than proximal. These unusual features are not shared, however, by FMNH P13000. An important feature of the ulnovolar surface of Mc IV is the weaker development than in *M. elatus* of ulnar and volar tubercles (Fig. 22H). There is, however, the same depression between the tubercles that occurs in *M. elatus*, and an Mc V facet is clearly developed and separated by a space from the proximal edge of the bone.

Only the proximal end of Mc V is preserved in CM 1424. The preserved part has a single cup-

shaped facet for Mc IV on its dorsoradial side. Distally the bone does not seem to diverge as far from Mc IV as does Mc V of *M. elatus*.

Hindlimb

A left femur and two damaged tibiae are preserved in the holotype, but these cannot be differentiated from specimens of *M. elatus*.

The holotype also preserves both astragali, and F:AM 54,902g (Fig. 23C) represents an additional specimen. In each, there is a distinct, short distal neck, similar to that in *M. elatus*. In dorsal aspect the three bones are similar to one another and to *M. elatus* in 1) the greater transverse width of the fibular side of the trochlea and its more gradual slope compared with the tibial side, 2) the somewhat greater proximal extension of the tibial side, and 3) the distal extension of the free part of the fibular side to the level of the distal articular facet. In the holotype the relief on the volar surface of the astragalus is considerably less than in F:AM 54,902g and in *M. elatus*. Its ectal facet is quite shallowly and uniformly concave, and the strong ridge separating the ectal facet proximally from the trochlea is straight (as in *M. elatus*) rather than curved. There is barely any eminence between the confluent ectal and calcaneal facets, and the sustentacular facet, weakly convex, is abruptly truncated at its almost straight proximofibular edge. Between the sustentacular and ectal facets is a broad but relatively shallow depression. In F:AM 54,902g the volar facets, while resembling in shape those of the holotype, have a very strong relief. The large ectal facet is especially deep in its distal part and is divided from the also slanted, contiguous calcaneal facet by a very sharp ridge. A deep but narrow groove separates the ectal from the sustentacular facet. A difference from both the holotype and *M. elatus* is the curved rather than straight proximal crest between the ectal facet and trochlea. All three astragali have a navicular facet on the distal surface very similar to that in *M. elatus*. In astragalus proportions there is a distinct dichotomy between *M. elatus* and *M. hollandi* on the one hand and all known later North American specimens (and also later Eurasian schizotheriines) on the other. *M. elatus* and *M. hollandi* are similar in that the proportion of tibial height/transverse width in all specimens (Table 4) falls between 0.72 and 0.81; in contrast, the later North American specimens have a lower value (range 0.61–0.66 for a total of four specimens). The decrease in the ratio in the later spec-



Fig. 27.—Dorsal views of A) right Mt III of *M. elatus*, AMNH 14.378, from the Agate Spring Quarries, Sioux Co., Nebraska. B) left Mt III of *M. hollandi*, FMNH P13000, from near Jay Em. Goshen Co., Wyoming, and C) left Mt III of *Moropus* cf. *M. hollandi*, F:AM 54,903, from near Jay Em. Goshen Co., Wyoming. Proximal (D, dorsal edge below), tibial (E), and volar (F) views of Mt III of *M. hollandi*, FMNH P13000. Facet abbreviations as in Fig. 16; X = broken surface; unlabeled line to Mt IV facet.

imens is related not only to genuine broadening of the bones relative to height but also to reductions in the neck (particularly in *Moropus merriami*) and a decrease in height of the tibial side of the trochlea relative to the fibular side.

On the two broken calcanea of the holotype the tuber calcis is relatively shorter than in *M. elatus*, and there is only a slight volar prominence at the end of the tuber. As might be expected from holotype astragali (above), the ectal facet is not so

strongly convex as in *M. elatus* and apparently does not extend so far onto the tuber. No facet for the tibia can be discerned in this individual. The sustentacular process is broken off, but the well-developed "lesser process" remains, separated by a sharp ridge from the cuboid facet on the distal surface. This latter facet is pear-shaped as in *M. elatus* but almost completely flat.

Two known cuboids resemble specimens of *M. elatus* and differ from *M. distans* and *M. merriami*

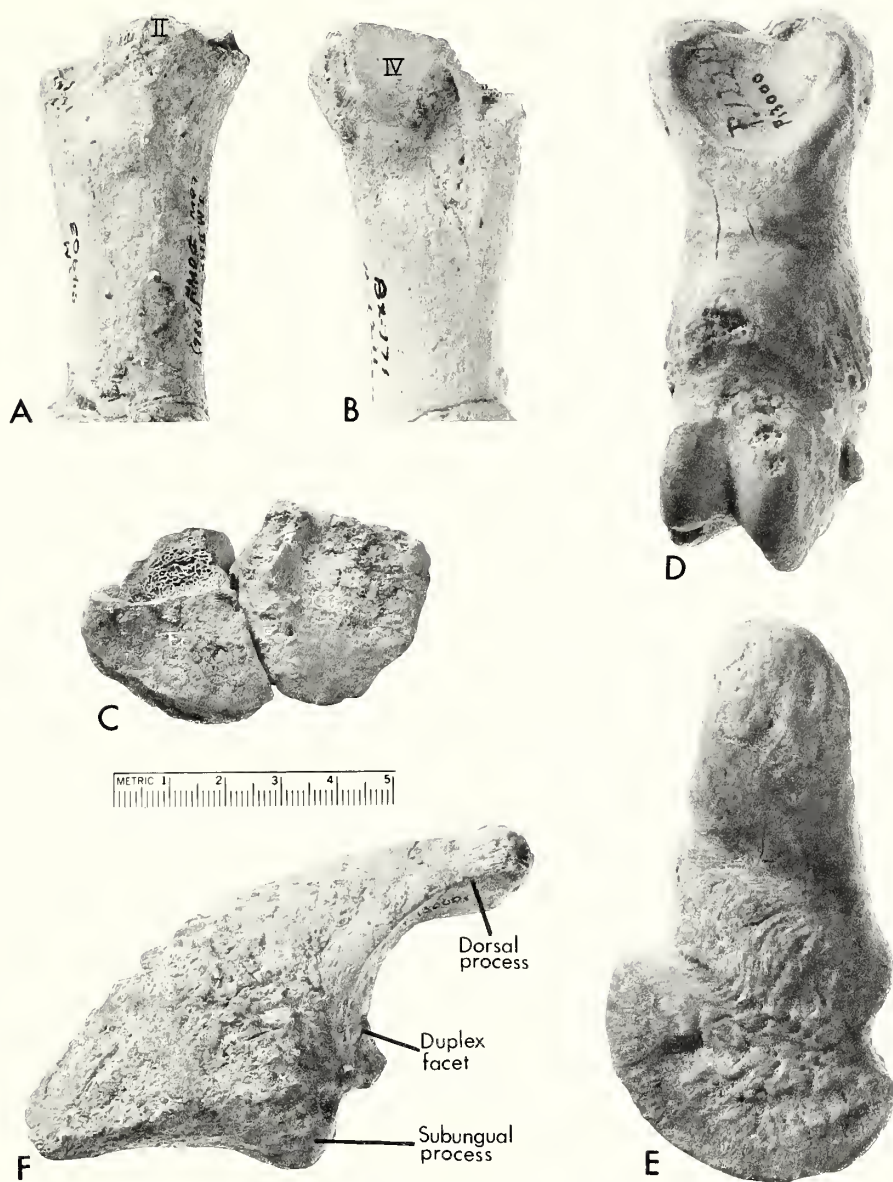


Fig. 28.—Tibial (A) and fibular (B) views of Mt III and proximal view (C) of Mt III and Mt IV (dorsal edge below) of F:AM 54,903, *Moropus* cf. *M. hollandi*. Dorsal (D) and ulnar (E) views of left duplex, and ungual phalanx (F) of digit II of the manus of FMNH P13000, a presumed female specimen of *M. hollandi*. All specimens from near Jay Em, Goshen Co., Wyoming. Facet abbreviations as in Fig. 16.

in the failure of the navicular facet to reach the proximal edge of the bone or to adjoin the calcaneum facet (Fig. 16A). Navicular and cuboid are thus separated at their proximal and volar edges by a small space. In this specimen dorsal and volar parts of the ectocuneiform facet are continuous and show no constriction between them, whereas in *M. elatus* the two parts of the facet are sometimes separate. The dorsal part of the ectocuneiform facet

extends distally to adjoin the Mt IV facet, but the volar part of the facet is well separated from the distal end of the cuboid. In this individual the tibiovascular process is not remarkably developed (Fig. 16A). A navicular of FMNH P13000 (Fig. 16G) falls easily within the range of morphology of *M. elatus* and cannot be differentiated in any special way.

No metatarsals are known from the type of *M. hollandi*, but FMNH P13000 preserves a Mt III

(Figs. 27B, D–F), which can be compared with Mt III and Mt IV of F:AM 54.903 (*Moropus* cf. *M. hollandi*, see Figs. 27C, 28A–C). Table 6 gives the length versus width proportions of metatarsals of *M. hollandi* and *M. elatus*. FMNH P13000 (Mt III) falls within the range of *M. elatus* in length/maximum distal width but has a lower length/minimum shaft width than most specimens of *M. elatus*. Apparently, broadening of the metatarsal shaft relative to length has proceeded in *M. hollandi* despite continued resemblance to *M. elatus* in many other respects. Mt III and Mt IV of F:AM 54.903 fall below the range of *M. elatus* in both proportions. Mt III of FMNH P13000 and F:AM 54.903 complement one another in preservation in that the proximal end of the former is broken at the dorsofibular angle, whereas that of the latter lacks the facets for Mt II and most of the volar part of the facet for Mt IV. The subtriangular, tibially slanted proximal facet, for the ectocuneiform (Fig. 27D), resembles its counterpart in *M. elatus*, as does the small bipartite Mt II facet (Fig. 27E), where it is preserved in FMNH P13000. In this specimen dorsal and volar parts of the Mt II facet are connected by a thin proximal articular platform. Facets for Mt IV differ between the two Mt III specimens. In FMNH P13000 the shape of the volar part of the facet suggests that it was discrete and well separated from the dorsal Mt IV facet (Fig. 27F). In F:AM 54.903 the two parts of the Mt IV facet are not only adjacent but are confluent at their most proximal edges (Fig. 28B). Further, the two parts of the facet in this latter specimen are more closely equal in size than in *M. elatus*; the situation in FMNH P13000 is not clear. Both specimens show more dorsal to volar compression of the shaft, especially toward the distal end, than occurs in *M. elatus*. This change seems to be concomitant with the shortening and broadening of the shaft.

Mt IV of F:AM 54.903 is slenderer and distinctly longer than Mt III of the same specimen, proportionately more so than in *M. elatus*. The greatest difference between this bone and specimens of *M. elatus* is the presence of one continuous facet rather than two facets on the tibial side of the proximal end, corresponding with facets on Mt III above. The two parts of the facet are of almost equal size (the dorsal part is slightly larger), and the connection between them begins at the crest dividing them from the cuboid facet and continues distally over half of the facet. In addition to this partial dorsal-volar division, there is a functional division into

proximal and distal parts, separated only by a barely visible ridge. The more proximal part of the facet, with a proximal to tibial orientation, articulates with the ectocuneiform (Fig. 28C), while the larger, more distal parts of the facet articulate with Mt III. There is strong development of the fibulovolar angle of the proximal end of this Mt IV, although not so strong as in *M. elatus*, and there is a weak longitudinal ridge on the fibular side of the shaft. The distal end of this specimen is clearly asymmetrical.

Phalanges

A single large duplex of digit II of the manus belonging to the holotype and two similar duplexes of FMNH P13000 (Figs. 28D, E) suggest by their size and morphology that both of these specimens are females, a conclusion consistent with the small size of these individuals compared to known males of *M. elatus*. The specimens are quite similar to those of female *M. elatus* in having a less flattened, more symmetrical Mc II facet than in *M. elatus* males. These duplexes are compressed transversely but thickened in the dorsal to volar direction, more so than is usual in *M. elatus*.

Additional proximal phalanges are available but add little to characterization of *M. hollandi*. Most of these appear to belong to digits III or IV of the manus, but one specimen, belonging to F:AM 54.902f, may belong to digit III or IV of the pes despite its unexpectedly large size. This specimen has a pronounced thickening of its volar part, remarkable because in this and other features it is extremely similar to F:AM 54.911 from Flint Hill Quarry in the Batesland Formation of South Dakota. The presence of *M. hollandi* in the early Hemingfordian fauna of the Batesland Formation is unclear, however, for other *Moropus* material from Flint Hill Quarry collected by the University of California shows no special resemblance to known specimens of *M. hollandi*. *M. hollandi* is not known from the roughly contemporaneous fauna of the Runningwater Formation of Nebraska.

Small medial and ungual phalanges of *M. hollandi* show no features of particular taxonomic interest. A large ungual phalanx belonging to FMNH P13000 (Fig. 28F) closely resembles the large ungual phalanx of digit II of the manus in *M. elatus* but is slenderer. Its dorsal and subungual processes are large, but the facet for the duplex is not deeply excavated and has only a weak keel dividing its two halves.

CONCLUSIONS AND ZOOGEOGRAPHY

The genus *Moropus* is derived relative to *Schizotherium* in its higher crowned and more elongated molar teeth, in the absence of a hypoconulid on M_3 , in the proportionate shortening of metatarsals, and in fusion of proximal and medial phalanges of digit II of the manus to form a duplex bone. Its closest relatives among the Schizotheriinae are *Phyllotillon*, *Ancylotherium*, and a yet unpublished genus of North American Miocene schizotheriine. These genera share the above characters with *Moropus*, but they are additionally derived in a number of others, for example, the presence in *Ancylotherium* and sometimes in *Phyllotillon* of a crochet and posterior labial rib on upper molars.

The four *Moropus* species discussed in this paper are all relatively primitive representatives of *Moropus*, little removed from the Eurasian/North American common stock of the genus (see Coombs, 1974). *M. distans*, the type species, is poorly known but includes *Moropus* individuals of relatively small size. Because the few available remains of *M. distans* include a duplex of digit II of the pes, it is possible that phalangeal fusion to form a pes duplex was more common in *M. distans* than in *M. elatus*. *M. distans* also differs from *M. elatus* but resembles *Moropus merriami* in the more proximal extent of its navicular facet on the cuboid. *Moropus oregonensis* is known only from upper premolars and molars, which are smaller than comparable teeth of *M. elatus* and differ in the manner of wear on upper premolars. *M. distans* may be synonymous with *M. oregonensis*, but no elements clearly linking the two species have yet been found. *Moropus senex*, known from a single specimen, shows no useful features for differentiating species and is therefore considered a *nomen dubium*.

Moropus elatus is the best known *Moropus* species and is the most useful basis for intrageneric and intergeneric comparisons. Male *M. elatus* are at the extreme high end of *Moropus* size range, and the molar teeth of *M. elatus* are slightly more elongated and high crowned than those of *M. oregonensis*. Yet *M. elatus* has otherwise diverged little from its common ancestry with *M. distans* and *M. oregonensis*. *Moropus hollandi* closely resembles *M. elatus* but differs in the loss or strong reduction of the trapezium in the manus and the dorsal to volar compression of certain other carpal elements. Loss of the trapezium occurs independently in *Schizotherium turgaicum*, *Borissiakia betpakdalen-*

sis and *Ancylotherium* (*Ancylotherium*) *pentelicum* but within *Moropus* is characteristic only of *M. hollandi*, where it presumably allowed increased flexion of the carpus. *M. hollandi* also has proportionately shortened its metatarsals relative to most of *M. elatus*, consistent with a general trend toward such shortening within the Schizotheriinae over time. On the basis of the above given similarities and differences, *Moropus elatus* and *M. hollandi* seem to be closely related, whereas *M. distans* and *M. oregonensis* may be closer to *M. merriami*. *Moropus merriami* and its kin will be more thoroughly discussed in a separate paper, as will *Moropus matthewi*.

It is difficult to discuss the zoogeography of early *Moropus* species on present scanty evidence. *M. distans* and *M. oregonensis* are known only from the late Arikareean of Oregon. *M. elatus* from the late Arikareean/early Hemingfordian of Nebraska, and *M. hollandi* from the early Hemingfordian of Nebraska and Wyoming. Contemporary materials from other areas are few and for the most part too fragmentary for taxonomic treatment. Scattered remains from Oregon to Florida do suggest a broad geographic range and probably a more complex early Miocene evolutionary story than can currently be reconstructed. *Moropus* is much more common in the fluvial channel fills in the base of the Upper Harrison Formation than in any other rock unit (Hunt, personal communication). This high rate of occurrence of *Moropus elatus* in particular could be a result of its relatively greater abundance or could be related to dietary, herding, or other habits that made them more liable to preservation. On the other hand, the conditions of deposition of the Upper Harrison Formation could have been unusually conducive to chalicotheres entombment.

The earliest documented occurrences of *Moropus* in North America are late Arikareean. At this time or somewhat earlier the genus apparently immigrated from Eurasia across the Bering land bridge or migrated southward as part of a hitherto unsampled northern Holarctic fauna. An Eurasian origin is supported by the absence of chalicotheres in North American Oligocene deposits and their presence in the Oligocene of Eurasia (*Oreinoitherium bilobatum* from the Oligocene of Saskatchewan is a brontothere, not a chalicotheres, as Skinner, 1968, also asserted), the presence of small *Moropus* sp. very similar to *M. elatus* in the European Aquitanian (Coombs, 1974), and the late Arikareean or early

Hemingfordian appearance in North America of other immigrants from Eurasia (see, for example, the amphicyonids *Cynelos* and *Ysengrinia* in Hunt, 1972, and the primitive deer *Blastomeryx* cited along with other genera by Wilson, 1967, 1968). Floral geography may also be correlated with the early Miocene appearance of *Moropus* in North America. Wolfe (1969b:85; 1972:230) suggested that the probably early Miocene Collawash flora from Oregon indicated that floristically the warm temperate vegetation at middle latitudes represented a Mixed Mesophytic forest for the first time. At that time the temperate, moist forests of both Oregon

and Alaska contained a number of common species and are considered part of the same floristic province (Wolfe, 1969a:91). Wolfe and Leopold (1967:195) also noted that early Miocene floras of Alaska contained a remarkable number of elements in common with both Oregon and Japan. It is very difficult to associate *Moropus* with any particular floral element, but its known North American late Arikareean distribution is quite similar to that of the tayassuid *Cynorca sociale*, whose range was correlated with floral information by Woodburne (1969).

ACKNOWLEDGMENTS

The cooperation of many people is reflected in the completion of this study, and the efforts of all are greatly appreciated. Drs. Bobb Schaeffer and Malcolm C. McKenna provided both advice and access to collections and archives at the American Museum of Natural History. I am especially indebted to Drs. Richard H. Tedford and Robert M. Hunt and Messrs. Morris F. Skinner, Ted Galusha, and Beryl E. Taylor for their time in imparting to me their first-hand knowledge of collecting areas and biostratigraphic correlations. Dr. Walter P. Coombs provided useful ideas throughout the evolution of this paper and was particularly helpful in preparing the photographic illustrations.

The following individuals provided access to collections and/or help in obtaining loans: Dr. Mary R. Dawson, Carnegie Museum of Natural History; Dr. William D. Turnbull and Ms. Kay

Krueger of the Field Museum of Natural History; Dr. Glenn L. Jepsen, Princeton University; Dr. Grant Meyer and Mr. James O. Farlow of the Peabody Museum of Natural History; Dr. Donald E. Savage and Dr. J. Howard Hutchison of the University of California Museum of Paleontology; and Drs. Leonard Ginsburg and Donald E. Russell of the Muséum National d'Histoire Naturelle, Paris.

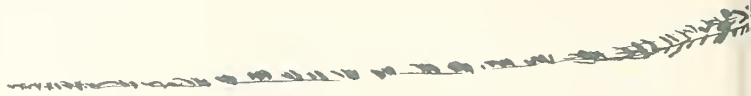
This study was supported in part by a faculty fellowship from Columbia University; my 1975 excavation at Morava Ranch Quarry was supported by a grant from the National Geographic Society, and examination of relevant specimens in European museums was supported by Grant No. GB-33496 from the National Science Foundation.

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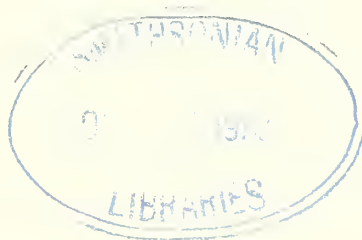
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BULLETIN

of CARNEGIE MUSEUM OF NATURAL HISTORY



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BIRDS ANALYZED BY MONTH, AGE, AND SEX

MARY H. CLENCH
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BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 5, pages 1-85

Issued 20 September 1978

Price \$5.00 a copy

Craig C. Black, Director

Editorial Staff:—Hugh H. Genoways, Publications Editor; Duane A. Schlitter, Associate Publications Editor; Stephen L. Williams, Associate Publications Editor; Teresa M. Bona, Technical Assistant.

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CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213

INTRODUCTION

In 1961 Carnegie Museum of Natural History initiated a bird-banding program at its field research station, Powdermill Nature Reserve. The Reserve is located in the Ligonier Valley, which at its latitude is the westernmost valley of the Allegheny Mountains. The banding station is approximately three miles south of Rector, Westmoreland County, Pennsylvania (40°10'N, 79°16'W).

The Powdermill program has concentrated primarily on the study of small land birds, by using 30- and 36-mm mesh mist nets; larger birds are sometimes captured in traps or in nets of larger mesh. During the banding procedure the following data are routinely recorded: band number, species, age and sex (when possible), date, time of day, wing chord measurement, fat index, and weight. Since the autumn of 1966, many of the passerines also have been examined for the degree of skull pneumatization, to determine age.

As the Powdermill program has become better known to the ornithological community, we have received many requests for data from our files, particularly for weights. The types of studies prompting these requests have been remarkably diverse. For example, bird weights are used by theoretical ecologists concerned with biomass calculations; by laboratory physiologists needing comparative data from normal wild birds; and, of course, by ornithologists and banders for taxonomic, zoogeographic, and many other types of studies.

Weight data also have some unexpected applications. For instance, we have been asked on two different occasions to supply British ornithologists with weights of common North American species. In both cases vagrant birds of North American origin had appeared in England and it was suspected that they might have reached those shores by "assisted passage" rather than having flown (or been blown) there on their own. Both vagrants had been weighed when they were found in England, but normal weights for migrating individuals of their species could not be located in the literature for comparison. Another unusual request for a bird weight came from an experimental engineer. During a test flight of a new jet airplane, a small bird had collided with the plane's windshield. The glass broke, the plane went out of control and crashed, with the pilots ejecting safely. The company that had developed the glass for the windshield asked us for the weight of the bird species involved. That figure was

critical for their calculations on the force that had broken the glass, in order to strengthen the windshield in the next model.

Although weights of many eastern North American species can be found in the literature, most represent single birds or small samples, often without full supporting data (date, locality, age, sex). Seldom have they represented sufficiently large samples to be useful to researchers. In addition, some of the published weights have been incidental to the main study and hence are difficult to locate from the paper's title. Weight data are also widely scattered through the literature. An incomplete manuscript bibliography of bird weights and their evolutionary interpretation compiled by G. A. Clark, Jr. in 1976 contains almost 600 titles gleaned from both ornithological and non-ornithological sources. Therefore, seeing a need for a compilation of adequate samples of the weights of North American birds, we present here an analysis of much of the data from the Powdermill program accumulated through the spring of 1974: 97,762 weights from 151 species.

All of the weights in this study are from living, banded birds. The birds are weighed, while being restrained in a sock or plastic cone, on a triple-beam balance. The scales are counterbalanced against the sock or cone and hence the weight of the bird alone is read directly, to the nearest 0.1 gram. The sex of the bird is recorded as M (male), F (female), or U (unknown). In species that are not sexually dimorphic in plumage, the sex of some individuals has been determined during the breeding season by the presence of a brood patch or cloacal protuberance, changes in eye or mouth color, etc.

The age designations are the same as those currently in use by the Bird Banding Laboratory, U.S. Fish & Wildlife Service: HY = a bird in its *hatching year*, up to 31 December in its first year of life; SY = *second year*, the calendar year after the bird was hatched; ASY = *after second year*; TY = *third year*; ATY = *after third year*; AHY = *after hatching year*, but precise age not known; and U = *unknown*, age not determined. Among the birds aged specifically SY through ATY, some have been thus recorded through plumage characteristics or skull pneumatization, but most are birds that were originally banded as HY and subsequently rehandled. Those recorded as age unknown are birds banded after the breeding season has begun and

before 31 December: primarily non-passerines that cannot be aged by skull pneumatization or plumage, passerines in which the skull may pneumatize early, and certain other autumn-banded passerines handled before 1966 when we first began to examine skulls routinely. A few birds were not recorded by age or sex inadvertently, or because they were in anomalous plumage.

Nomenclature follows *The A.O.U. Check-list of North American Birds* (American Ornithologists' Union, 1957) and *Supplements* (Auk 90: 411–419, 1973 and Auk 93: 875–879, 1976). Included in the list of species is one composite, "Traill's Flycatcher." This name includes the Alder and Willow flycatchers, which cannot safely be distinguished in the hand. Also in the list are several hybrid types such as "Brewster's Warbler" and "Lawrence's Warbler."

The sample sizes range from one (eight species) to 7,715 (Dark-eyed Junco). We have included the very small samples because even though they represent only one or two birds, they may well be the only, or among the very few, published weights for those species (e.g., Least Bittern, Boreal Chickadee). The weights are analyzed by age/sex class by month. In the smaller samples the data are arranged linearly as follows:

Sample size in parentheses (N); age/sex class; month; weight in grams (means of two or more weights italicized).

The larger samples are arranged in table groups:

(N)	sample size
Mean	weight to 0.1 grams, italicized
[1 standard deviation]	in samples of 5 or more
Minimum weight in sample	weight range within sample
Maximum weight in sample	

Note that the 97,762 weights here recorded are not from 97,762 different birds. Most of the birds are, of course, weighed only once—at the time of banding. But the study also includes many thousands of birds that have been weighed several times: migrants that are recaptured within a few hours or days of banding, and resident birds that are repeatedly captured throughout their lifetime. Each recapture weight has been included in its appropriate category. For example, if a Black-capped Chickadee were banded and weighed as an HY-U in September, then were recaptured the following June and could be sexed as a male from its cloacal protuberance, its recapture weight would be entered in the SY-M category for June, and the original weight

in the HY-M September category. Known age birds were carried through their third year (TY) in detail, and then grouped as ATY thereafter.

The reader will notice that the standard deviation values for many samples are large. These reflect several factors: weights can vary greatly during the breeding season (a female with a mature egg will weigh well above the mean), and the contents of the stomach and gut have a strong effect on the overall live weight (a thrush that has just filled its stomach with wild cherries, with pits, will weigh considerably more than a newly arrived migrant of the same species that has not yet fed). Whether or not a bird has recently defecated also has some effect, but most birds do so during the handling process and before they are weighed. The most important variable that affects weight is the quantity of fat deposits within the body and under the skin. To illustrate the effect of fat, we cite the extreme case of a recently handled migrant Cape May Warbler: the bird was banded as an HY-F in September with no visible fat (index of 0) and weighing 9.2 grams (10.0 is the mean for that category). It was recaptured several weeks later, with maximum fat (index 3) and weighing 15.8 grams—a 72% gain over the original weight. Resident birds, in contrast, show little weight and fat index variation. A Tufted Titmouse that has been weighed 16 times over a ten-year period has only varied between 19.3 and 21.4 grams, always with a fat index of 0 or 1.

Although we are well aware that the weight of a bird is biologically more meaningful when related to the fat index of that bird, we did not attempt to include fat indices in this analysis. With a possible 21 different age/sex classes, analyzed by the 12 months of the year, some species could yield a table with 252 groups. Breaking the age/sex classes further into the four fat index classifications (0–3) would be too unwieldy for a study of this sort. Detailed analysis of weight variation is also more meaningful when correlated with each individual's body size, but similarly, such a fragmentation would be inappropriate for this study. The Powdermill banding records are, however, being entered into an electronic data processing system and analyses of weight by fat index and/or body size class could be made in the future. We are also, of course, continually adding data to our files at the rate of over 10,000 per year. Requests for special analyses may be possible to fill: address the Section of Birds, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213.

ACKNOWLEDGMENTS

A study of this magnitude has had many contributors. First and foremost we thank A. C. Lloyd for his many years of devoted service as a volunteer in the Powdermill banding program. We also thank the dozens of people, too many to name individually, who have helped in a variety of ways with the banding since 1961, and the several clerks who have kept our banding records. This analysis was largely accomplished by two research assistants: Dr. Gail Schiffer, who began the data compilation and statistical work, and Mr. G. Thomas Bancroft, who

saw the task to completion and ran most of the analyses on the University of Pittsburgh computer. Marilyn Niedermeier volunteered to copy the results into a uniform format for typing. She was assisted in proof reading by Thomas E. Herman and Miriam A. Stern. Cynthia Kraus typed the manuscript. The assistance of Dr. Schiffer and Mr. Bancroft was supported by the Powdermill Research Fund through the generosity of Mrs. Cordelia S. May.

Pied-billed Grebe	<i>Podilymbus podiceps</i>										n = 3	
(1) HY-U, Sept., 429.4; (1) AHY-U, Sept., 341.1; (1) U-U, Oct., 229.0.												
Green Heron	<i>Butorides striatus</i>										n = 5	
(1) HY-U, July, 186.8; (1) HY-U, Sept., 171.2; (1) HY-U, Oct., 210.6; (1) AHY-U, June, 236.7; (1) SY-U, June, 215.2.												
Least Bittern	<i>Ixobrychus exilis</i>										n = 1	
(1) AHY-U, May, 115.5.												
Goshawk	<i>Accipiter gentilis</i>										n = 1	
(1) HY-U, Nov., 444.5.												
Sharp-shinned Hawk	<i>Accipiter striatus</i>										n = 12	
(1) HY-F, Oct., 159.2; (1) HY-M, Sept., 91.0; (1) HY-U, Sept., 93.0; (1) HY-U, Nov., 115.8; (1) AHY-M, Apr., 101.5; (1) SY-F, Apr., 184.1; (2) SY-M, Apr., 92.2, 97.3 (94.8); (1) SY-U, Apr., 102.5; (1) ASY-M, Mar., 88.5; (1) ASY-U, Apr., 100.9; (1) ASY-U, Nov., 101.8.												
Broad-winged Hawk	<i>Buteo platypterus</i>										n = 4	
(3) AHY-U, Apr., 311.2, 452.2, 472.2 (411.9); (1) AHY-U, May, 360.7.												
Ruffed Grouse	<i>Bonasa umbellus</i>										n = 3	
(1) HY-U (poult), July, 171.7; (1) AHY-F, July, 516.3; (1) AHY-M, Oct., 506.8.												
Bobwhite	<i>Colinus virginianus</i>										n = 1	
(1) AHY-M, May, 162.7.												
Virginia Rail	<i>Rallus limicola</i>										n = 2	
(1) AHY-U, Apr., 79.5; (1) AHY-U, May, 90.2.												
Sora	<i>Porzana carolina</i>										n = 3	
(2) HY-U, Sept., 77.8, 84.2 (81.0); (1) AHY-U, May, 85.0.												
American Woodcock	<i>Philohela minor</i>										n = 34	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(4) 160.6 139.3 179.4	(2) 183.0 179.4 186.6		
HY-M								(1) 141.0	(2) 142.4 127.2 157.6	(2) 155.4 135.4 175.5	(1) 159.0	
HY-U								(1) 142.2		(1) 191.5		
AHY-F				(1) 200.0	(1) 200.5				(2) 191.7 184.7 198.7	(1) 187.6		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-M			(1) 134.3	(2) 123.2 116.1 130.4	(4) 151.2 135.1 183.1					(1) 152.4		
AHY-U				(2) 130.6 127.3 133.9	(1) 111.8							
U-U									(2) 153.9 144.7 163.1	(2) 169.4 134.4 204.4		

Common Snipe

Capella gallinago

n = 5

(1) HY-U, Oct., 125.4; (1) AHY-U, Mar., 96.0; (1) AHY-U, Apr., 118.6; (1) U-U, Sept., 110.8; (1) U-U, Oct., 125.4.

Spotted Sandpiper

Actitis macularia

n = 46

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U				(6) 40.6 [3.53] 35.5 44.6	(32) 39.9 [4.95] 32.8 53.1		(2) 39.9 33.8 46.0					
U-U							(1) 39.6	(2) 37.0 33.7 40.2	(3) 54.6 46.1 59.8			

Solitary Sandpiper

Tringa solitaria

n = 6

(2) AHY-U, Apr., 48.1, 56.9 (52.5); (3) AHY-U, May, 46.2, 52.6, 53.4 (50.7); (1) U-U, Sept., 60.7.

Pectoral Sandpiper

Calidris melanotos

n = 1

(1) HY-U, Sept., 44.8.

Mourning Dove

Zenaida macroura

n = 16

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F			(2) 140.3 138.1 142.5	(1) 130.8	(3) 128.1 119.7 132.5							
AHY-M		(1) 126.5	(2) 138.0 135.2 140.9	(1) 135.0	(3) 136.7 128.7 143.3	(1) 134.0						
AHY-U				(1) 122.1	(1) 160.0							

Yellow-billed Cuckoo

Coccyzus americanus

n = 90

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(2) 42.4 41.3 43.5	(2) 50.8 50.2 51.4	(1) 74.3		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F						(1) 55.7						
AHY-M						(1) 53.6						
AHY-U					(40) 64.5 [8.62] 52.0 81.5	(27) 70.8 [8.04] 51.0 84.6			(5) 60.1 [6.79] 50.5 68.0	(3) 55.1 50.0 61.2		
U-U									(2) 55.3 54.2 56.4	(6) 56.6 [5.78] 48.7 63.6		

Black-billed Cuckoo

Coccyzus erythrophthalmus

n = 71

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(5) 39.1 [2.25] 35.1 40.5	(1) 44.4	(3) 46.3 44.3 49.8	(2) 51.6 46.4 56.8		
AHY-F					(1) 64.4			(1) 52.8				
AHY-M					(1) 53.4							
AHY-U					(35) 51.8 [6.15] 40.9 63.2	(9) 53.4 [7.79] 44.2 64.9	(1) 49.9	(1) 43.4				
U-U								(4) 45.7 41.5 55.5	(1) 47.8	(6) 52.6 [7.60] 41.8 61.2		

Screech Owl

Otus asio

n = 9

(1) HY-U, Sept., 140.1; (2) AHY-U, Mar., 154.3, 170.3 (162.3); (1) AHY-U, Apr., 160.8; (1) AHY-U, May, 165.9; (3) U-U, Sept., 153.3, 157.9, 166.6 (159.3); (1) U-U, Nov., 176.0.

Saw-whet Owl

Aegolius acadicus

n = 7

(2) HY-U, Nov., 74.5, 88.4 (81.4); (1) AHY-U, Mar., 72.6; (1) AHY-U, Apr., 90.8; (1) AHY-U, Oct., 81.7; (1) U-U, Oct., 97.6; (1) U-U, Nov., 87.3.

Whip-poor-will

Caprimulgus vociferus

n = 4

(1) HY-F, Sept., 51.4; (1) AHY-M, May, 56.5; (1) AHY-M, Aug., 54.6; (1) U-U, Sept., 55.4.

Chimney Swift

Chaetura pelagica

n = 2

(2) U-U, Sept., 19.5, 21.3 (20.4).

Ruby-throated Hummingbird

Archilochus colubris

n = 1312

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(6) 3.1 [0.30] 2.8 3.6	(120) 3.3 [0.28] 2.6 4.0	(130) 3.4 [0.37] 2.6 4.4			
HY-M							(8) 3.1 [0.20] 2.8 3.4	(147) 3.0 [0.28] 2.4 4.0	(161) 3.2 [0.40] 2.4 4.7			
HY-U							(1) 3.3	(22) 3.2 [0.43] 2.6 4.2	(13) 3.2 [0.22] 2.9 3.6			
AHY-F					(167) 3.3 [0.28] 2.7 4.7	(19) 3.3 [0.26] 2.9 3.8	(32) 3.3 [0.40] 2.7 4.8	(112) 3.3 [0.36] 2.7 4.5	(89) 3.5 [0.38] 2.7 4.8			
AHY-M				(3) 3.1 3.0 3.2	(135) 3.0 [0.34] 2.4 4.1	(11) 2.7 [0.24] 2.5 2.8	(5) 2.8 [0.00] 2.7 2.8	(43) 3.2 [0.28] 2.5 3.9	(5) 3.2 [0.14] 3.0 3.4			
U-F								(46) 3.3 [0.30] 2.8 4.0	(24) 3.5 [0.40] 2.8 4.4			
U-U								(7) 3.0 [0.14] 2.8 3.3	(6) 3.5 [0.53] 3.0 4.3			

Belted Kingfisher

Megasceryle alcyon

n = 26

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(1) 133.5			
AHY-F					(3) 149.7 137.0 156.3	(1) 135.9						
AHY-M					(1) 137.4		(1) 136.5					
U-F							(1) 140.9	(4) 134.9 124.6 140.8	(6) 156.0 [16.37] 139.5 186.5			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-M								(1) 136.8	(5) 135.5 [11.56] 126.5 155.0	(2) 171.7 170.8 172.6		
Common Flicker (Yellow-shafted Flicker)								<i>Colaptes auratus</i>		n = 167		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 138.5	(1) 113.3	(1) 141.7		
HY-M								(2) 129.8 125.2 134.3	(1) 141.4			
HY-U								(2) 127.8 125.2 130.5				
AHY-F			(2) 127.4 117.4 137.5	(30) 127.0 [9.72] 106.2 154.6	(7) 129.3 [6.19] 119.0 135.6	(1) 110.1	(1) 126.3					
AHY-M	(1) 148.3		(3) 129.1 113.9 149.2	(38) 136.1 [10.12] 117.7 160.2	(13) 132.2 [6.20] 120.7 140.8	(1) 137.0	(2) 134.1 125.1 143.1					
U-F									(12) 129.8 [10.74] 111.5 143.3	(12) 135.1 [12.98] 110.1 163.7		
U-M								(8) 127.3 [6.45] 120.6 138.1	(15) 136.3 [9.57] 122.2 159.0	(11) 140.3 [9.75] 124.1 152.2	(2) 134.4 127.0 141.8	

Pileated Woodpecker

Dryocopus pileatus

n = 4

(1) AHY-F, Apr., 269.6; (2) AHY-F, May, 250.3, 275.1 (262.7); (1) U-U, Nov., 248.1.

Red-bellied Woodpecker

Melanerpes carolinus

n = 2

(1) SY-M, Jan., 80.3; (1) ASY-F, May, 74.5.

Yellow-bellied Sapsucker

Sphyrapicus varius

n = 60

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(4) 51.8 45.2 59.3	(6) 50.3 [1.98] 47.3 53.0		

1978

CLENCH AND LEBERMAN—PENNSYLVANIA BIRD WEIGHTS

11

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M									(4) 49.7 45.6 52.4	(5) 52.6 [2.91] 48.4 55.8		
HY-U									(2) 48.0 45.5 50.4	(3) 48.0 44.0 50.6		(1) 51.1
AHY-F				(4) 51.4 46.5 57.1	(1) 47.7				(1) 52.0	(1) 46.2		
AHY-M				(14) 50.5 [5.75] 40.7 62.2					(2) 51.8 51.2 52.3			
AHY-U				(1) 51.6								
SY-F				(1) 44.2								
SY-M				(3) 54.6 48.5 59.2								
ASY-F				(4) 49.5 46.2 54.7								
ASY-M				(3) 45.3 45.1 45.6								

Hairy Woodpecker

Picoides villosus

n = 51

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 56.2			(1) 65.1	
HY-M							(2) 65.2 62.2 68.1		(3) 73.5 73.1 74.0	(3) 69.1 67.6 70.4		
HY-U								(1) 72.0		(1) 67.0		
AHY-F		(1) 65.9	(2) 61.3 60.6 62.0		(3) 60.6 59.3 62.5	(3) 63.5 61.9 65.6			(1) 63.2			
AHY-M	(1) 74.6	(1) 69.9		(7) 67.5 [5.88] 60.8 75.5	(5) 73.6 [3.91] 69.0 79.6			(1) 64.1		(1) 70.2		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-F											(1) 63.2	
U-M									(3) 71.2 65.0 74.7	(6) 69.0 [2.10] 66.6 72.8	(2) 71.5 71.2 71.8	
U-U								(1) 69.1				
Downy Woodpecker <i>Picoides pubescens</i> n = 560												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F						(1) 24.1	(5) 24.5 [0.99] 23.6 25.7	(7) 26.4 [2.09] 23.6 29.3	(16) 26.7 [1.14] 24.0 28.3	(15) 27.2 [1.16] 24.2 28.8	(7) 27.6 [1.14] 26.5 29.3	
HY-M							(6) 25.7 [1.28] 24.3 27.5	(11) 26.4 [0.71] 25.2 27.7	(21) 27.4 [1.37] 25.0 31.3	(20) 27.6 [1.37] 24.9 29.6	(14) 26.9 [2.45] 23.4 32.1	
HY-U						(3) 25.1 23.1 26.2	(18) 25.0 [1.36] 22.8 27.6	(22) 26.0 [1.18] 23.7 28.6	(6) 27.0 [1.74] 24.6 29.3	(3) 27.2 26.3 27.6		
AHY-F	(6) 27.1 [1.87] 24.1 29.2	(2) 28.2 27.1 29.2	(18) 28.0 [1.76] 25.5 30.9	(38) 27.2 [1.51] 24.1 31.6	(15) 27.3 [1.54] 25.2 30.6	(2) 25.8 25.4 26.1	(2) 25.4 24.6 26.2	(4) 26.2 25.0 26.7	(4) 26.8 25.0 30.1	(11) 27.3 [1.81] 25.4 30.3	(12) 26.8 [1.61] 24.8 30.1	(3) 28.7 26.4 30.7
AHY-M	(3) 26.6 25.1 27.9	(2) 25.9 25.7 26.1	(25) 27.4 [1.60] 25.1 31.5	(44) 27.0 [1.34] 24.4 29.8	(34) 27.4 [1.89] 20.7 30.3	(7) 25.7 [1.29] 23.4 26.8		(6) 26.9 [1.04] 25.6 28.1	(7) 26.3 [1.51] 24.6 28.2	(18) 26.9 [1.47] 23.6 30.0	(10) 28.1 [1.69] 25.6 31.3	
AHY-U				(1) 25.2								
SY-F		(1) 26.8		(1) 28.9								
SY-M				(2) 25.2 21.9 28.5	(3) 29.0 27.4 31.5							
U-F								(2) 27.4 25.9 29.0	(12) 26.7 [1.33] 24.0 28.9	(19) 27.7 [1.51] 26.0 32.2	(5) 26.5 [1.41] 24.3 28.0	(2) 27.0 25.9 28.1
U-M									(17) 26.9 [1.88] 23.5 31.4	(29) 26.0 [2.47] 21.8 30.9	(14) 27.1 [2.91] 21.2 30.3	(3) 26.2 23.8 28.5

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-U									(1) 28.9			
Eastern Kingbird						<i>Tyrannus tyrannus</i>					n = 28	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(10) 39.3 [3.14] 34.5 44.4	(5) 41.7 [3.19] 37.8 45.4			
AHY-U					(9) 39.8 [1.16] 37.4 40.8			(3) 40.7 39.0 43.4				
U-U								(1) 42.0				
Great Crested Flycatcher						<i>Myiarchus crinitus</i>					n = 40	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(2) 32.4 32.1 32.8	(1) 36.8			
AHY-U					(9) 33.1 [2.38] 29.7 36.9	(9) 34.5 [2.71] 30.8 38.6	(1) 34.3	(8) 33.5 [3.67] 28.0 39.5	(5) 33.1 [2.00] 31.2 35.7			
U-U								(4) 33.6 32.2 35.0	(1) 33.1			
Eastern Phoebe						<i>Sayornis phoebe</i>					n = 485	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U						(6) 18.3 [1.46] 16.8 20.6	(15) 17.8 [1.62] 14.0 20.3	(32) 18.6 [1.47] 15.5 21.6	(57) 19.5 [1.59] 16.2 22.8	(41) 19.6 [2.61] 11.3 23.5		
AHY-F					(3) 19.1 18.1 20.5	(1) 19.4	(1) 19.5					
AHY-M			(3) 24.0 23.2 24.4	(1) 23.2	(1) 22.4	(1) 20.0						
AHY-U			(28) 19.8 [1.82] 16.6 23.6	(63) 19.8 [1.70] 16.1 24.3	(15) 20.1 [1.02] 18.3 21.6	(2) 20.8 20.6 21.0		(35) 19.8 [1.78] 16.0 23.2	(18) 19.4 [0.68] 18.0 20.5			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-U						(1) 16.5		(1) 18.4	(39) 19.6 [1.80] 13.3 23.0	(118) 19.7 [1.81] 11.4 23.8	(3) 20.8 19.6 21.6	

Yellow-bellied Flycatcher

Empidonax flaviventris

n = 505

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M									(1) 12.2			
HY-U								(99) 11.2 [0.89] 8.9 13.2	(226) 11.2 [0.90] 9.2 14.3	(10) 11.9 [1.44] 10.0 13.8		
AHY-F					(1) 12.7							
AHY-M					(2) 12.2 11.9 12.5			(1) 9.2				
AHY-U					(106) 11.5 [0.90] 9.5 13.9	(5) 11.6 [0.97] 10.5 12.9		(14) 12.1 [1.27] 10.2 14.8	(14) 11.9 [1.45] 9.6 15.5	(1) 11.8		
U-U							(1) 11.8	(4) 11.8 10.8 13.6	(20) 11.2 [0.92] 9.7 12.9			

Acadian Flycatcher

Empidonax virescens

n = 102

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(3) 12.7 12.1 13.7	(21) 13.0 [1.03] 11.5 15.4	(15) 13.0 [1.01] 11.1 14.7	(1) 12.5		
AHY-F							(1) 13.2					
AHY-U					(52) 12.9 [1.11] 10.4 16.1	(3) 12.7 12.5 12.9		(4) 12.2 9.8 14.4	(1) 13.5			
U-U								(1) 12.4				

"Traill's" Flycatcher

Empidonax traillii and *E. alnorum*

n = 302

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(73) 12.7 [1.00] 10.5 15.0	(54) 14.5 [2.07] 10.2 19.5	(3) 14.7 12.6 15.8		
AHY-F							(1) 12.4	(2) 11.8 11.7 12.0				
AHY-M					(1) 11.6	(1) 13.5						
AHY-U					(110) 13.5 [1.33] 9.2 16.9	(14) 12.9 [0.89] 11.4 14.4	(3) 13.3 11.1 16.0	(28) 13.4 [0.80] 11.2 14.8	(3) 13.9 13.2 14.8			
U-U									(9) 13.2 [1.69] 10.8 15.7			

Least Flycatcher

Empidonax minimus

n = 1289

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(6) 9.2 [0.61] 8.3 10.0	(397) 10.1 [0.93] 8.2 14.1	(461) 10.3 [0.90] 7.6 15.6	(12) 10.7 [0.71] 8.1 11.8		
AHY-F					(10) 10.3 [0.97] 8.9 12.6		(4) 9.7 9.0 10.1	(4) 9.3 8.6 9.9	(7) 9.3 [0.56] 8.7 10.4			
AHY-U				(6) 10.6 [0.72] 9.5 11.4	(257) 10.3 [0.85] 8.2 12.3	(3) 10.6 10.2 10.9	(14) 10.8 [0.61] 9.8 11.6	(35) 10.3 [0.93] 8.6 13.4	(44) 10.3 [1.15] 8.4 14.9	(1) 8.6		
U-U								(9) 9.8 [0.54] 8.8 10.5	(18) 10.1 [0.71] 8.5 11.0	(1) 13.2		

Eastern Wood Pewee

Contopus virens

n = 455

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(1) 12.9	(92) 13.0 [0.89] 10.6 15.2	(212) 13.3 [1.09] 11.0 18.7	(15) 14.2 [1.01] 12.6 16.5		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(2) 15.2 14.8 15.6		(1) 14.0					
AHY-U					(38) 14.3 [0.95] 12.8 16.5	(11) 13.1 [0.70] 12.2 14.3	(6) 14.0 [0.73] 12.8 14.8	(30) 13.8 [1.07] 12.2 16.4	(35) 14.5 [1.27] 12.3 18.2	(2) 15.7 13.3 18.1		
U-U								(1) 12.5	(8) 12.8 [1.23] 10.4 14.1	(1) 14.0		

Olive-sided Flycatcher

Nuttallornis borealis

n = 43

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(7) 30.4 [2.01] 28.6 34.6	(10) 31.3 [1.91] 27.8 34.0			
AHY-U					(8) 33.0 [5.16] 27.9 42.2			(6) 32.2 [2.94] 29.6 36.5	(4) 32.7 31.3 33.9			
U-U								(2) 27.5 26.7 28.3	(4) 32.0 31.3 33.0	(2) 32.0 29.9 34.0		

Tree Swallow

Iridoprocne bicolor

n = 28

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F				(2) 20.0 19.5 20.5	(4) 18.6 15.6 20.9							
AHY-M				(8) 21.5 [1.55] 19.0 23.3	(10) 19.3 [1.28] 17.4 21.3							
AHY-U				(1) 22.6	(3) 19.9 17.1 22.2							

Bank Swallow

Riparia riparia

n = 22

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U				(6) 14.6 [0.53] 13.8 15.3	(16) 13.0 [1.41] 9.9 15.3							

Rough-winged Swallow

Stelgidopteryx ruficollis

n = 47

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(4) 15.6 14.2 17.2							
AHY-M				(1) 16.2	(2) 16.4 16.0 16.7							
AHY-U				(7) 16.6 [1.02] 15.3 18.0	(33) 15.8 [1.52] 10.3 18.3							

Barn Swallow

Hirundo rustica

n = 178

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(5) 19.0 [1.61] 17.7 21.1	(7) 18.7 [0.84] 17.7 20.0	(7) 19.6 [1.34] 17.3 21.6			
AHY-F				(7) 19.0 [1.66] 16.8 21.1	(39) 18.1 [1.93] 13.4 23.4							
AHY-M				(5) 20.2 [1.95] 17.8 22.5	(54) 18.6 [1.55] 15.5 21.7							
AHY-U				(7) 18.9 [1.78] 15.6 20.7	(44) 18.6 [1.86] 13.7 22.8							
ASY-F					(1) 20.0							
ATY-F					(1) 20.9							
ATY-M				(1) 18.3								

Cliff Swallow

Petrochelidon pyrrhonota

n = 3

(1) HY-U, Aug., 22.6; (1) AHY-U, Apr., 25.5; (1) AHY-U, May, 18.5.

Blue Jay

Cyanocitta cristata

n = 515

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(3) 85.3 80.3 87.9	(12) 85.6 [6.65] 74.7 97.5	(27) 87.3 [5.22] 77.7 96.6	(8) 87.0 [5.32] 79.7 94.4	(3) 89.2 86.8 92.1

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F											(1) 90.4	
AHY-U	(5) 89.2 [4.73] 82.2 94.6	(9) 86.0 [6.45] 77.1 96.0	(12) 88.0 [3.74] 81.8 95.4	(8) 85.6 [5.06] 79.5 96.0	(18) 83.8 [6.55] 73.1 97.5				(12) 90.3 [4.14] 83.5 96.2	(16) 88.4 [8.47] 64.1 99.0	(7) 89.6 [4.43] 85.5 97.2	(6) 91.3 [6.01] 81.7 99.5
SY-F					(1) 79.1							
SY-U	(13) 85.4 [7.70] 69.0 97.1	(5) 79.7 [6.45] 74.4 90.9	(27) 85.3 [5.57] 75.6 101.2	(43) 86.7 [6.24] 76.1 97.7	(112) 85.2 [6.24] 72.8 99.7				(2) 82.4 80.5 84.4	(3) 88.1 82.7 94.3	(2) 90.8 90.5 91.1	
ASY-F		(1) 87.4			(1) 86.3					(1) 90.9		
ASY-M				(1) 79.4								
ASY-U	(9) 90.2 [7.23] 81.1 104.2	(7) 86.4 [7.68] 77.4 95.9	(26) 89.5 [5.74] 76.3 101.4	(41) 88.5 [6.55] 76.2 101.1	(62) 86.6 [6.15] 74.6 102.9	(1) 92.3			(1) 109.4	(1) 101.3	(4) 92.8 83.9 98.0	(1) 77.9
U-U										(1) 84.4		(2) 89.8 88.5 91.2

Common Crow

Corvus brachyrhynchos

n = 1

(1) HY-U, Aug., 411.5.

Black-capped Chickadee

Parus atricapillus

n = 3307

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(1) 10.5		(3) 10.6 10.0 11.3	(3) 10.4 9.8 10.8	(5) 10.4 [0.32]	
HY-M								(1) 10.9	(5) 11.2 [0.55] 10.8 12.2	(6) 11.2 [0.58] 10.6 12.2	(2) 11.5 11.4 11.6	
HY-U						(3) 9.7 8.9 10.4	(70) 10.3 [0.71] 8.2 11.9	(118) 10.7 [0.77] 8.9 12.6	(199) 10.7 [0.78] 8.9 12.5	(726) 10.5 [0.75] 8.3 13.5	(280) 10.7 [0.75] 8.7 12.7	(5) 10.5 [0.65] 9.8 11.4
AHY-F			(2) 10.2 10.1 10.3		(3) 10.3 9.9 10.8	(1) 9.6						
AHY-M	(3) 10.9 10.9 11.0	(2) 10.9 10.7 11.1	(3) 11.2 10.7 11.6	(2) 10.8 10.4 11.1	(6) 10.8 [0.54] 10.2 11.3	(1) 10.6			(1) 11.6		(1) 11.0	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U	(84) <i>10.8</i> [0.79] 9.5 13.0	(55) <i>10.9</i> [0.84] 9.2 12.6	(158) <i>11.0</i> [0.80] 9.2 13.0	(231) <i>10.9</i> [0.84] 9.2 13.2	(28) <i>10.8</i> [0.80] 9.1 12.4		(4) <i>10.2</i> 9.2 10.8	(8) <i>10.6</i> [0.52] 9.6 11.4	(15) <i>10.6</i> [0.56] 10.0 11.8	(51) <i>10.5</i> [0.79] 8.9 12.8	(45) <i>10.8</i> [0.79] 9.5 12.5	(4) <i>10.5</i> 9.9 11.2
SY-F			(8) <i>10.2</i> [0.52] 9.3 11.0	(3) <i>10.7</i> 10.2 11.3	(2) <i>10.7</i> 10.4 10.9					(3) <i>10.3</i> 9.7 10.8	(1) <i>10.3</i>	
SY-M			(9) <i>11.7</i> [0.33] 11.2 12.2	(3) <i>11.6</i> 11.3 12.2	(5) <i>11.4</i> [0.45] 10.8 12.0	(1) <i>12.0</i>		(1) <i>12.3</i>	(3) <i>11.2</i> 10.9 11.6	(3) <i>10.8</i> 10.0 11.2	(6) <i>11.3</i> [0.47] 10.6 11.9	
SY-U	(38) <i>10.9</i> [0.92] 8.9 12.5	(7) <i>10.7</i> [0.48] 9.8 11.3	(83) <i>11.0</i> [0.72] 9.5 12.6	(34) <i>11.2</i> [1.05] 9.2 12.9	(7) <i>11.3</i> [0.33] 10.8 11.9			(3) <i>10.7</i> 10.5 10.9	(10) <i>10.8</i> [0.77] 9.2 12.0	(18) <i>10.9</i> [0.91] 9.0 12.2	(13) <i>10.9</i> [0.72] 9.9 12.0	(1) <i>11.3</i>
ASY-F	(2) <i>10.2</i> 9.9 10.5		(2) <i>11.1</i> 10.7 11.5	(5) <i>11.2</i> [0.55] 10.6 11.8	(1) <i>11.4</i>				(2) <i>10.3</i> 10.0 10.6			
ASY-M			(5) <i>11.4</i> [0.23] 11.2 11.7	(2) <i>10.9</i> 10.3 11.5	(3) <i>11.1</i> 10.7 11.5				(1) <i>10.6</i>	(1) <i>11.0</i>	(2) <i>10.5</i> 10.2 10.9	
ASY-U	(20) <i>11.1</i> [0.64] 9.9 12.4	(8) <i>11.1</i> [1.02] 9.5 12.0	(42) <i>11.1</i> [0.77] 9.4 12.6	(24) <i>11.1</i> [0.86] 9.6 12.7	(1) <i>11.0</i>			(1) <i>11.2</i>	(2) 9.6 9.5 9.7	(3) 9.8 8.2 10.9	(7) <i>10.5</i> [0.70] 9.4 11.5	(2) <i>11.0</i> 10.9 11.0
TY-F		(1) <i>10.9</i>	(2) <i>10.5</i> 10.3 10.6								(1) <i>10.1</i>	
TY-M		(1) <i>11.6</i>	(5) <i>11.4</i> [0.47] 10.8 11.9	(4) <i>11.4</i> 10.5 11.9	(1) <i>11.8</i>				(1) <i>11.7</i>	(2) <i>10.9</i> 10.4 11.3		
TY-U	(9) <i>11.6</i> [0.83] 10.1 12.7		(18) <i>11.5</i> [0.65] 10.6 12.8	(8) <i>11.3</i> [0.89] 10.3 13.1	(2) <i>10.9</i> 10.7 11.1		(1) 8.8	(1) <i>12.3</i>	(2) <i>10.6</i> 10.5 10.7	(4) <i>11.0</i> 10.3 11.6	(5) <i>10.4</i> [1.00] 9.0 11.6	
ATY-F	(1) <i>10.8</i>	(1) <i>10.4</i>	(1) <i>10.8</i>		(1) <i>10.9</i>					(1) <i>10.0</i>		
ATY-M	(2) <i>11.3</i> 11.2 11.3		(5) <i>11.3</i> [0.38] 10.8 11.8	(1) <i>11.5</i>	(1) <i>10.3</i>					(2) <i>10.9</i> 10.4 11.4	(1) <i>10.5</i>	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
ATY-U	(15) <i>10.5</i> [0.76] 9.3 11.8	(7) <i>10.8</i> [0.70] 9.9 12.0	(57) <i>11.0</i> [0.81] 9.3 13.0	(34) <i>10.8</i> [0.79] 9.5 12.5	(3) <i>11.4</i> 11.3 11.5			(2) <i>10.9</i> 9.8 12.1 12.3	(6) <i>10.8</i> [0.44] 10.1 11.4	(9) <i>10.3</i> [0.92] 8.9 11.6	(13) <i>10.0</i> [0.70] 8.8 11.1	(3) <i>10.9</i> 10.4 9.5 12.3	
U-U							(3) <i>10.5</i> 10.1 10.8	(13) <i>10.4</i> [0.83] 9.1 12.3	(64) <i>10.5</i> [0.83] 9.0 12.7	(290) <i>10.6</i> [0.71] 8.8 13.6	(134) <i>10.9</i> [0.79] 8.6 12.7	(36) <i>10.9</i> [0.67] 9.5 12.3	
Carolina Chickadee						<i>Parus carolinensis</i>						n = 15	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
HY-U							(1) <i>9.8</i>		(1) <i>9.5</i>	(5) <i>9.0</i> [0.22] 8.7 9.3	(1) <i>9.6</i>		
AHY-U			(1) <i>10.1</i>	(1) <i>9.8</i>									
SY-U	(2) <i>9.2</i> 9.1 9.4	(2) <i>9.4</i> 9.4	(1) <i>9.9</i>										
Boreal Chickadee						<i>Parus hudsonicus</i>						n = 1	
(1) AHY-U, Oct., 9.7.													
Tufted Titmouse (Eastern Tufted Titmouse)						<i>Parus bicolor</i>						n = 1314	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
HY-F								(1) <i>20.5</i>	(1) <i>23.3</i>	(1) <i>20.4</i>	(2) <i>22.7</i> 22.5 22.8	(1) <i>20.8</i>	
HY-M							(1) <i>22.3</i>			(1) <i>23.0</i>		(1) <i>23.7</i>	
HY-U						(7) <i>21.4</i> [1.28] 19.2 23.5	(38) <i>20.4</i> [1.44] 17.6 24.0	(50) <i>21.5</i> [1.58] 18.7 25.0	(101) <i>21.8</i> [1.55] 18.3 25.8	(176) <i>21.7</i> [1.68] 16.7 27.5	(98) <i>21.9</i> [1.42] 18.5 24.6	(7) <i>22.2</i> [1.37] 20.0 23.6	
AHY-F	(1) <i>20.1</i>		(5) <i>20.5</i> [0.31] 20.1 20.9	(4) <i>21.2</i> 19.6 22.2	(7) <i>22.0</i> [1.33] 20.3 24.6						(2) <i>21.1</i> 20.4 21.8		
AHY-M				(1) <i>22.5</i>									
AHY-U	(33) <i>22.4</i> [1.60] 18.7 25.5	(29) <i>21.7</i> [1.50] 19.3 24.3	(109) <i>22.0</i> [1.80] 18.0 27.0	(74) <i>21.5</i> [1.78] 17.2 25.5	(17) <i>21.6</i> [1.35] 19.2 23.5		(1) <i>19.6</i>	(1) <i>19.4</i>		(10) <i>21.7</i> [1.37] 19.5 24.0	(18) <i>21.2</i> [1.34] 18.9 24.8	(1) <i>23.8</i>	

1978

CLENCH AND LEBERMAN—PENNSYLVANIA BIRD WEIGHTS

21

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
SY-F	(1)	(1)	(5)	(3)	(3)						(2)	
	20.7	20.9	21.1	21.5	23.0						20.7	
			[0.80]	20.7	21.1						20.4	
			19.9	22.1	24.6						21.0	
			22.1									
SY-M			(1)		(1)							
			22.2		21.7							
SY-U	(23)	(8)	(53)	(44)	(15)				(6)	(14)	(31)	(1)
	22.4	22.3	22.7	22.7	22.2				21.7	22.3	21.7	21.9
	[1.22]	[0.95]	[1.67]	[1.37]	[0.96]				[1.80]	[1.60]	[1.40]	
	20.3	20.3	17.7	19.0	20.7				19.4	19.5	17.4	
	24.9	23.3	26.0	25.3	23.9				24.0	24.6	24.7	
ASY-F			(1)									
			21.6									
ASY-M					(1)						(1)	
					22.1						23.0	
ASY-U	(2)	(2)	(18)	(12)	(8)	(1)				(9)	(10)	(4)
	23.3	22.6	23.0	22.4	22.2	23.1				21.6	22.1	21.2
	23.1	22.4	[1.45]	[1.62]	[1.39]					[1.16]	[1.56]	20.6
	23.5	22.7	19.7	19.6	20.8					19.5	19.9	22.1
			25.2	25.5	24.6					23.7	24.2	
TY-U	(6)	(3)	(13)	(9)	(7)				(1)	(9)	(3)	(1)
	22.9	21.4	21.7	22.9	22.6				22.2	21.5	21.6	22.3
	[4.00]	21.2	[2.32]	[1.36]	[0.83]					[1.47]	20.2	
	17.4	21.7	18.3	19.8	21.6					18.7	24.0	
	29.3		26.0	24.1	24.2					23.5		
ATY-F		(1)									(1)	
		20.4									21.7	
ATY-M			(2)		(3)				(1)			
			22.3		22.6				22.1			
			21.4		22.0							
			23.2		23.0							
ATY-U	(5)	(5)	(26)	(17)	(4)					(2)	(12)	
	22.7	22.3	22.5	22.3	21.3					21.8	21.7	
	[1.62]	[1.27]	[1.14]	[1.74]	20.4					21.0	[1.22]	
	20.7	21.3	20.5	20.5	22.4					22.6	20.3	
	25.0	24.5	25.1	27.2							24.5	
U-F										(1)	(3)	
										21.1	20.7	
											20.2	
											21.2	
U-U							(1)	(2)	(29)	(22)	(34)	(11)
							23.3	21.2	21.7	22.2	21.4	22.7
								20.3	[1.52]	[1.87]	[1.24]	[1.30]
								22.0	19.5	19.3	18.5	21.3
									24.9	28.9	24.2	24.8

White-breasted Nuthatch

Sitta carolinensis

n = 296

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 20.7	(1) 18.4	(7) 20.7 [1.38] 19.2 23.3	(2) 20.3 20.1 20.5	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(2) 19.8 19.5 20.1	(3) 21.9 20.2 23.2		(7) 20.8 [0.53] 19.9 21.2	(6) 21.2 [1.36] 19.2 22.8	(1) 21.7
AHY-F	(4) 21.0 19.4 22.0	(5) 20.6 [1.24] 19.4 22.3	(16) 21.0 [0.96] 19.4 22.8	(7) 21.4 [1.30] 19.0 23.2	(1) 21.1		(1) 20.7			(8) 20.8 [1.33] 19.0 22.4	(5) 20.7 [0.55] 19.8 21.2	(1) 20.4
AHY-U	(6) 22.0 [0.99] 20.7 23.0	(4) 22.5 20.1 24.6	(38) 21.3 [1.42] 18.8 24.4	(26) 20.4 [1.30] 18.5 22.8	(3) 21.1 20.7 21.4	(2) 20.3 19.5 21.1	(2) 20.0 19.7 20.4		(1) 17.2	(11) 21.2 [0.74] 20.2 22.4	(11) 21.6 [0.70] 20.2 22.7	(1) 21.1
SY-F	(1) 19.8		(1) 21.3	(2) 21.8 21.2 22.3					(1) 20.6			
SY-U	(1) 21.8		(6) 21.7 [0.52] 20.8 22.2	(2) 21.2 20.0 22.4							(3) 21.5 20.1 22.2	(1) 23.0
ASY-F	(2) 21.1 20.2 21.9	(1) 21.9	(3) 21.8 20.6 22.7	(2) 20.2 19.3 21.0						(3) 21.0 20.4 22.2	(4) 21.5 20.3 22.6	
ASY-U	(1) 20.1		(9) 21.7 [2.06] 19.2 26.7	(5) 21.3 [0.50] 20.5 21.8						(1) 21.3	(4) 22.6 20.7 23.9	
TY-U			(1) 21.7									
ATY-F			(1) 20.5					(1) 19.6	(1) 20.4	(1) 20.6		
ATY-U			(3) 21.0 20.3 22.2	(3) 21.1 20.0 22.1		(1) 21.3						
U-F										(2) 21.3 20.1 22.4	(8) 20.6 [0.92] 19.2 22.0	(1) 21.7
U-U									(5) 21.0 [0.92] 19.8 22.3	(11) 21.6 [0.87] 19.7 22.6	(15) 21.4 [0.72] 20.0 22.8	(6) 22.2 [0.65] 21.6 23.3

Red-breasted Nuthatch

Sitta canadensis

n = 7

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M										(1) 12.1		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(2) 10.5 10.1 10.8			
AHY-F										(2) 10.6 10.4 10.8	(2) 11.2 10.7 11.6	
Brown Creeper												
											n = 152	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U						(1) 7.5		(3) 7.6 7.1 8.4	(2) 8.6 8.2 9.0	(19) 8.2 [0.43] 9.1	(15) 7.9 [0.65] 7.0 8.9	
AHY-F					(1) 8.0				(1) 8.0			
AHY-U			(19) 8.3 [0.46] 7.4 9.1	(26) 8.5 [0.66] 7.2 9.7						(19) 8.3 [0.56] 7.2 9.3	(6) 8.6 [0.66] 7.4 9.3	
SY-U			(1) 7.9	(1) 8.1								
ASY-U			(1) 8.2									
ATY-U											(1) 8.7	
U-U									(3) 8.2 8.1 8.4	(25) 8.3 [0.61] 7.4 9.9	(8) 8.3 [0.51] 7.7 9.3	
House Wren												
											n = 1055	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U						(2) 10.4 9.7 11.0	(76) 10.3 [0.48] 8.5 11.4	(178) 10.7 [0.75] 8.0 13.3	(345) 11.1 [0.84] 9.2 14.5	(107) 11.4 [0.74] 9.6 13.2	(1) 12.5	
AHY-F					(6) 10.5 [0.58] 9.9 11.5	(2) 12.2 11.1 13.2	(5) 11.5 [0.64] 10.9 12.5	(6) 11.4 [0.69] 10.7 12.3				
AHY-M					(5) 10.9 [0.60] 10.4 11.9	(1) 10.9	(2) 10.7 10.5 10.8		(1) 10.8			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U				(24) 10.7 [0.68] 9.7 12.2	(87) 10.6 [0.83] 8.9 14.2	(2) 11.1 11.0 11.2	(13) 11.0 [0.26] 10.5 11.5	(30) 11.2 [0.79] 9.9 12.6	(29) 11.3 [0.78] 9.7 13.8	(13) 11.2 [0.95] 9.7 13.1		
SY-U					(3) 10.6 10.1 11.2		(1) 9.7					
ASY-F					(1) 13.2	(3) 11.8 11.2 12.1						
ASY-M					(1) 10.8							
ASY-U				(3) 10.8 10.2 11.5	(4) 10.6 9.5 11.4							
ATY-F					(1) 11.7	(1) 10.2		(1) 10.9				
ATY-U				(1) 11.8	(2) 11.2 11.0 11.4							
U-M							(1) 11.0					
U-U							(3) 10.6 10.2 11.0	(22) 11.0 [0.67] 9.9 12.5	(64) 11.1 [0.86] 9.4 13.0	(8) 11.1 [1.05] 10.1 12.9		
<i>Troglodytes troglodytes</i>												
Winter Wren											n = 171	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(14) 8.6 [0.92] 7.2 10.1	(85) 8.9 [0.84] 7.1 10.7	(18) 9.1 [0.70] 8.1 10.3	
AHY-U			(1) 9.3	(8) 8.7 [0.52] 7.7 9.5	(1) 9.3				(2) 9.2 8.6 9.8	(28) 9.0 [0.78] 7.5 10.1	(1) 8.3	
U-U										(9) 8.7 [0.84] 7.7 10.1	(4) 9.0 7.8 10.5	
<i>Thryomanes bewickii</i>												
Bewick's Wren											n = 3	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U			(1) 9.2	(1) 11.3					(1) 11.3			

Carolina Wren

Thryothorus ludovicianus

n = 43

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(8) 18.7 [1.08] 17.3 20.3	(13) 18.6 [1.02] 16.6 20.2	(5) 17.6 [1.46] 15.6 19.2	(3) 19.7 17.7 21.6	(1) 20.3	
AHY-U			(1) 17.5	(3) 19.6 18.2 22.3	(3) 19.2 15.9 21.0	(1) 16.8	(1) 22.1		(1) 16.8			
SY-U			(3) 19.3 19.1 19.6									

Long-billed Marsh Wren

Cistothorus palustris

n = 35

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(10) 11.9 [1.25] 9.9 13.7	(15) 11.2 [1.15] 9.5 13.6		
AHY-U					(3) 12.7 11.5 13.5				(4) 11.3 10.1 12.1			
U-U									(2) 9.8 9.5 10.1	(1) 9.4		

Short-billed Marsh Wren

Cistothorus platensis

n = 3

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(2) 9.2 8.9 9.5	(1) 8.4		

Mockingbird

Mimus polyglottos

n = 2

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U				(2) 49.8 47.7 52.0								

Gray Catbird

Dumetella carolinensis

n = 3530

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(2) 36.3 35.0 37.5					
HY-M								(1) 39.0				

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U						(2) 31.4 30.7 32.0	(154) 35.4 [1.96] 29.3 41.5	(333) 36.4 [2.16] 30.0 43.4	(1028) 38.6 [2.85] 31.5 48.3	(271) 41.2 [3.40] 32.8 52.0	(3) 37.8 36.8 39.6	
AHY-F					(14) 35.0 [2.55] 30.9 40.9	(19) 36.9 [2.40] 33.4 40.7	(13) 37.8 [2.74] 33.9 42.2	(19) 36.3 [2.45] 33.3 41.7	(6) 39.6 [2.49] 35.4 42.8	(3) 38.5 32.2 46.0		
AHY-M					(12) 35.7 [4.40] 30.0 48.4	(17) 35.4 [1.14] 33.2 37.2	(5) 35.9 [0.80] 35.0 37.1	(3) 37.1 35.5 39.8	(1) 40.1			
AHY-U				(11) 34.5 [2.37] 32.1 40.7	(711) 34.8 [2.54] 26.7 45.2	(72) 34.7 [2.28] 26.6 40.6	(49) 36.2 [1.87] 32.1 40.2	(44) 37.6 [2.68] 32.1 43.7	(157) 40.0 [3.04] 30.5 47.7	(59) 43.5 [4.37] 34.3 56.5		
SY-F							(2) 35.3 30.3 40.3	(3) 33.6 31.2 35.7		(1) 41.7		
SY-M					(3) 32.1 30.1 34.5	(1) 34.6		(2) 35.5 34.2 36.8				
SY-U					(14) 34.4 [2.13] 31.3 39.7		(2) 37.3 33.5 41.1	(3) 39.1 38.4 39.6	(6) 41.3 [3.37] 37.1 45.5	(1) 45.5		
ASY-F					(1) 32.5	(1) 43.5	(2) 37.3 34.0 40.6	(1) 34.3	(1) 37.3			
ASY-M					(5) 34.7 [1.10] 33.5 36.1	(2) 35.0 34.3 35.6	(3) 34.5 33.1 36.1	(1) 42.4				
ASY-U					(18) 35.4 [1.60] 33.1 38.1	(1) 38.2		(3) 39.1 34.0 41.8	(2) 39.7 38.2 41.2	(1) 48.1		
TY-F					(2) 36.2 33.9 38.5			(1) 32.1		(1) 38.2		
TY-M					(3) 31.7 31.0 32.1			(1) 35.9	(1) 39.7			

1978

CLENCH AND LEBERMAN—PENNSYLVANIA BIRD WEIGHTS

27

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
TY-U					(1) 35.9	(2) 33.3 31.1 35.5	(1) 35.4	(2) 39.8 37.5 42.0	(3) 39.0 38.7 39.6			
ATY-F					(2) 35.3 34.4 36.2							
ATY-M					(8) 34.3 [1.18] 33.4 37.0	(1) 38.3						
ATY-U					(10) 36.0 [1.53] 33.5 38.1	(2) 33.4 33.3 33.5		(3) 37.3 35.3 41.1	(7) 39.6 [1.61] 36.5 41.1			
U-M								(1) 38.7				
U-U								(7) 37.7 [1.74] 35.9 39.7	(320) 39.3 [2.91] 32.3 47.9	(62) 40.7 [3.14] 31.5 49.0		
Brown Thrasher					<i>Toxostoma rufum</i>					n = 273		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(10) 66.4 [4.25] 58.2 74.1	(17) 68.9 [5.17] 60.0 78.6	(47) 69.8 [4.01] 62.0 80.6	(22) 72.5 [6.75] 55.1 92.2		
AHY-F				(2) 68.4 67.1 69.7	(9) 67.8 [2.97] 62.1 71.6	(2) 67.7 67.2 68.2	(2) 66.0 66.0 66.0	(1) 71.4				
AHY-M					(2) 72.8 62.5 83.0	(2) 67.8 66.2 69.3						
AHY-U				(61) 66.6 [5.39] 57.6 79.2	(40) 67.1 [5.82] 58.5 79.2	(2) 66.7 65.9 67.4		(3) 66.3 61.0 70.1	(15) 75.6 [6.26] 66.3 89.0	(2) 63.5 58.1 68.9		
ASY-U					(1) 66.3							
U-U									(22) 73.5 [5.01] 62.3 83.4	(11) 71.2 [4.04] 65.8 78.5		

American Robin		<i>Turdus migratorius</i>										n = 745
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 82.0	(1) 82.8	(12) 78.8 [6.16] 66.7 88.8	(2) 70.7 66.7 74.6	
HY-M									(1) 74.0	(16) 79.8 [5.86] 70.5 94.5	(3) 75.6 72.1 81.6	
HY-U					(3) 75.8 68.3 85.4	(9) 76.1 [3.87] 67.3 81.4	(61) 74.9 [4.97] 54.2 84.2	(51) 75.7 [3.55] 68.8 82.0	(7) 79.3 [5.94] 69.2 86.1	(41) 77.3 [4.66] 66.2 87.7	(19) 82.7 [5.06] 74.4 90.5	
AHY-F			(26) 77.8 [5.55] 70.8 94.4	(85) 77.2 [7.06] 63.5 102.6	(37) 79.8 [5.44] 69.5 88.5	(8) 78.8 [4.63] 70.4 86.1	(7) 76.1 [3.48] 70.9 80.4	(2) 81.5 80.3 82.7				
AHY-M			(37) 77.2 [5.59] 70.6 94.3	(76) 77.1 [6.34] 66.0 94.4	(57) 75.6 [5.55] 66.6 93.9	(9) 76.6 [4.94] 67.3 82.5		(1) 71.6		(4) 81.9 79.5 84.6		
AHY-U	(1) 81.0		(16) 76.6 [4.40] 68.1 85.3	(15) 77.3 [7.52] 66.4 94.0	(5) 76.4 [6.97] 69.6 86.4							
SY-F					(1) 88.9							
SY-U				(3) 75.4 71.0 78.4	(1) 68.6							
ASY-F			(1) 77.1	(3) 80.8 78.3 85.0	(1) 79.5	(1) 85.9						
ASY-M			(4) 75.6 71.3 80.1	(7) 70.4 [4.52] 64.2 78.1	(4) 77.1 75.0 78.7							
TY-U					(1) 77.4							
ATY-F				(2) 75.2 71.7 78.7						(1) 70.2		
ATY-M			(1) 68.8	(6) 73.0 [4.81] 65.1 79.8	(3) 76.7 70.9 84.1	(1) 74.5				(1) 76.0		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-F										(7) 81.8 [5.16] 75.7 90.0		
U-M										(4) 82.2 79.7 83.7	(4) 85.5 77.4 93.2	
U-U									(8) 79.8 [3.93] 73.5 85.3	(51) 79.1 [5.32] 67.7 94.4	(16) 82.3 [7.90] 65.6 97.5	

Wood Thrush

Hylocichla mustelina

n = 478

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(17) 47.8 [3.67] 39.3 52.6	(28) 50.4 [2.77] 42.8 54.2	(116) 50.6 [3.03] 40.1 58.4	(9) 52.7 [4.83] 44.0 60.6		
AHY-F					(8) 49.1 [1.38] 46.6 50.7	(6) 53.3 [2.55] 51.1 57.7	(7) 48.6 [3.08] 42.8 53.1	(1) 51.4				
AHY-M				(1) 45.4 [1.50] 42.1 47.4	(14) 45.4 [2.06] 42.3 48.5	(7) 46.0 [0.72] 47.2 49.0	(5) 48.0 [1.78] 45.0 53.3	(1) 50.1 [2.56] 46.9 54.2	(1) 45.6			
AHY-U				(5) 46.6 [4.58] 40.0 52.2	(123) 46.9 [3.41] 39.2 56.4	(9) 48.7 [3.06] 46.2 55.5	(7) 48.7 [1.78] 45.0 53.3	(4) 49.3 [2.56] 46.9 54.2	(7) 49.6 [2.56] 46.9 54.2	(1) 54.2		
SY-F					(5) 50.3 [3.13] 45.0 53.3	(3) 49.7 49.3 50.3	(1) 46.2					
SY-M					(6) 48.1 [3.50] 43.6 51.3	(2) 47.7 46.7 48.7	(1) 48.6					
SY-U				(5) 45.9 [2.98] 42.5 50.7	(34) 46.6 [2.90] 40.5 55.1	(2) 47.4 45.6 49.1	(2) 45.4 43.1 47.7					
ASY-F					(1) 46.8							

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-M				(1) 45.1	(7) 44.2 [1.93] 41.3 46.5	(1) 47.0	(1) 48.3					
ASY-U				(1) 45.1	(1) 44.1							
TY-U				(2) 47.8 47.0 48.5	(3) 45.7 45.5 46.0							
ATY-F					(1) 44.7	(1) 50.4						
ATY-M				(1) 50.6	(3) 47.4 45.6 48.6							
ATY-U					(1) 42.5							
U-M									(1) 49.2			
U-U									(14) 50.0 [2.91] 45.7 55.2			

Hermit Thrush

Catharus guttatus

n = 546

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(6) 29.1 [1.91] 26.7 31.6	(440) 30.6 [2.31] 24.6 39.8	(30) 32.3 [2.64] 28.9 39.6	
AHY-U				(3) 28.7 26.6 30.3	(4) 30.4 26.6 33.6				(1) 30.0	(29) 31.4 [2.14] 27.6 37.4	(1) 34.4	
SY-U				(5) 31.0 [2.12] 27.9 33.4	(5) 31.5 [1.25] 30.0 33.2							
U-U										(22) 30.7 [1.67] 27.5 34.0		

Swainson's Thrush

Catharus ustulatus

n = 2174

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(1) 31.6	(3) 30.5 26.4 33.3	(1036) 30.8 [2.54] 21.7 46.7	(112) 33.0 [3.81] 26.5 48.2		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F							(1) 31.1	(8) 29.6 [1.39] 28.0 32.1				
AHY-U				(3) 29.6 27.6 31.1	(249) 29.8 [2.68] 21.9 39.3	(4) 32.8 29.6 37.0	(2) 29.7 29.6 29.8	(14) 30.8 [1.70] 27.4 33.5	(119) 32.4 [2.96] 26.2 42.1	(10) 34.4 [3.54] 28.7 39.1		
SY-U				(1) 25.1	(82) 29.7 [2.70] 25.2 39.0							
U-U								(7) 29.2 [0.98] 28.1 30.5	(475) 30.8 [2.82] 24.7 50.7	(47) 35.1 [5.15] 26.5 47.7		
Gray-cheeked Thrush					<i>Catharus minimus</i>					n = 464		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(2) 33.1 31.8 34.4	(159) 32.1 [2.58] 25.0 40.8	(97) 36.5 [5.37] 25.4 52.6		
AHY-U					(22) 33.1 [3.34] 27.0 39.6				(37) 33.6 [3.91] 27.1 45.1	(9) 38.2 [5.98] 30.2 45.0		
SY-U					(2) 34.4 33.2 35.6							
U-U									(115) 31.6 [2.77] 26.4 39.8	(21) 35.3 [5.65] 27.2 50.5		
Veery					<i>Catharus fuscescens</i>					n = 116		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(11) 30.8 [1.63] 28.6 34.1	(33) 33.9 [4.06] 28.7 48.2			
AHY-F							(2) 30.7 30.3 31.0	(1) 29.1				

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U					(38) 31.0 [2.68] 26.3 35.8		(4) 28.8 26.2 31.7		(6) 34.8 [5.84] 29.2 41.7			
SY-U					(15) 31.0 [2.65] 27.9 37.8							
U-U									(6) 31.8 [3.14] 27.9 36.3			

Eastern Bluebird										<i>Sialia sialis</i>			n = 21	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.		
HY-M										(1) 29.4				
HY-U											(1) 40.0			
AHY-F			(4) 29.9 26.9 31.6	(1) 29.9	(1) 30.4					(1) 30.2	(1) 30.5			
AHY-M			(4) 29.7 27.5 32.0	(1) 28.9	(2) 29.7 28.4 30.9	(1) 29.3								
AHY-U			(1) 30.1											
U-F											(2) 31.8 30.7 32.8			

Blue-gray Gnatcatcher					<i>Poliophtila caerulea</i>								n = 235	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.		
HY-M								(1) 5.7						
HY-U							(10) 6.0 [0.22] 5.6 6.3	(36) 6.0 [0.26] 5.5 6.6	(4) 6.0 5.9 6.2					
AHY-F				(42) 5.8 [0.41] 4.8 6.8	(27) 6.4 [0.87] 5.4 8.9	(4) 6.5 6.1 7.0	(4) 5.9 5.2 6.4	(15) 6.0 [0.40] 5.3 6.7	(1) 5.9					
AHY-M				(36) 6.0 [0.37] 5.2 6.8	(19) 6.1 [0.28] 5.7 6.7	(3) 6.3 5.9 6.6	(2) 6.3 6.1 6.4	(3) 6.0 5.3 7.0						

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U				(2) 5.6 5.5 5.6	(1) 6.3	(1) 6.2	(1) 6.2	(6) 5.8 [0.67] 5.0 6.7				
SY-M						(1) 5.8						
ASY-M				(1) 6.0			(1) 6.2	(1) 6.2				
TY-M					(2) 6.0 5.9 6.1							
ATY-M				(1) 6.0	(1) 5.8			(1) 5.9				
U-U							(1) 6.1	(4) 6.2 5.0 6.7	(3) 6.2 6.1 6.4			

Golden-crowned Kinglet

Regulus satrapa

n = 643

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F										(55) 6.3 [0.58] 5.2 7.8	(51) 6.2 [0.44] 5.1 7.3	
HY-M									(1) 5.8	(63) 6.4 [0.50] 5.6 7.6	(65) 6.4 [0.43] 5.4 7.4	
AHY-F			(4) 5.6 5.5 5.8	(47) 5.8 [0.40] 5.1 7.1						(8) 6.4 [0.31] 6.1 6.9		
AHY-M	(4) 5.9 5.9 6.0		(21) 6.0 [0.40] 5.2 7.2	(104) 6.1 [0.44] 4.9 7.2						(8) 6.5 [0.54] 5.5 7.4	(5) 6.2 [0.46] 5.5 6.8	
SY-M			(1) 6.1									
U-F										(26) 6.2 [0.37] 5.4 6.7	(59) 6.3 [0.56] 4.5 7.8	(3) 5.8 5.9
U-M										(35) 6.5 [0.53] 5.6 7.6	(83) 6.4 [0.56] 5.3 7.7	

Ruby-crowned Kinglet

Regulus calendula

n = 3184

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(108) 6.3 [0.63] 4.9 8.5	(290) 6.3 [0.56] 5.2 8.3	(11) 6.8 [0.38] 6.2 7.5	
HY-M									(9) 6.7 [0.74] 5.6 8.1	(202) 6.8 [0.62] 5.5 8.6	(27) 7.1 [0.67] 5.9 9.5	
HY-U										(6) 6.2 [0.45] 5.6 6.8	(1) 6.7	
AHY-F				(118) 6.1 [0.37] 5.3 7.0	(338) 6.3 [0.47] 5.2 7.8				(33) 6.3 [0.47] 5.3 7.3			
AHY-M			(3) 6.6 6.5 6.7	(518) 6.8 [0.53] 5.4 8.9	(51) 7.1 [0.50] 5.9 8.6				(7) 6.7 [0.43] 6.0 7.4	(1) 6.0		
AHY-U				(3) 6.3 6.2 6.4	(2) 6.3 5.5 7.1							
U-F									(39) 6.4 [0.72] 5.3 8.0	(460) 6.5 [0.60] 5.1 8.9	(106) 6.6 [0.54] 5.1 8.3	
U-M									(5) 6.8 [0.63] 6.2 7.7	(610) 6.9 [0.61] 5.0 9.7	(229) 7.1 [0.54] 5.8 8.9	
U-U										(7) 6.8 [0.59] 6.1 7.8		

Cedar Waxwing

Bombycilla cedrorum

n = 3318

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 31.5				
HY-U							(7) 29.8 [1.58] 27.1 31.3	(506) 31.6 [2.26] 21.3 38.3	(675) 32.6 [2.14] 26.7 38.5	(248) 33.6 [2.12] 28.5 44.7	(89) 33.6 [2.48] 28.5 39.7	(3) 33.6 28.5 39.7

[illegible]

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-M					(1) 82.5							
U-U	(1) 82.2										(1) 77.0	

<i>Vireo griseus</i>												n = 88
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(5) 11.3 [0.42] 10.7 11.8	(4) 11.8 10.7 12.8			
AHY-F					(1) 11.9	(1) 12.7						
AHY-U				(9) 10.5 [0.52] 9.6 11.2	(49) 11.2 [0.71] 10.0 13.1	(5) 11.7 [0.55] 10.9 12.3	(4) 11.1 10.6 12.3	(3) 12.0 11.5 12.4	(3) 11.8 10.3 13.0		(1) 12.5	
ASY-F				(1) 11.4								
ASY-M					(1) 12.4	(1) 12.5						

<i>Vireo flavifrons</i>												n = 10
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(3) 18.3 16.7 19.4			
AHY-F							(1) 19.2					
AHY-U					(3) 15.7 15.0 17.0		(1) 17.2	(1) 16.1				
U-U									(1) 18.8			

<i>Vireo solitarius</i>												n = 114
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(42) 16.9 [1.30] 14.3 20.5	(49) 16.5 [0.93] 14.0 19.5		
AHY-U				(1) 15.1	(3) 16.7 15.6 18.4				(6) 16.5 [1.14] 14.7 17.7	(8) 16.9 [0.64] 16.0 18.2		
U-U										(4) 16.0 14.5 18.0	(1) 16.0	

Red-eyed Vireo

Vireo olivaceus

n = 2055

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(1) 16.7					
HY-M								(4) 16.6 16.0 17.3	(1) 15.8			
HY-U							(15) 17.1 [1.01] 15.5 18.6	(211) 16.7 [1.39] 11.5 23.1	(401) 17.3 [1.63] 12.2 25.7	(17) 18.9 [2.11] 17.0 23.7		
AHY-F					(16) 15.7 [0.92] 14.6 17.7	(24) 17.5 [1.42] 15.6 21.5	(64) 16.4 [0.92] 14.2 18.4	(51) 16.7 [1.14] 13.5 20.7	(7) 17.3 [0.76] 15.7 17.8			
AHY-M					(15) 16.5 [1.46] 14.2 19.6	(25) 16.7 [0.80] 15.5 18.3	(15) 16.7 [0.86] 14.6 18.2	(18) 16.9 [1.32] 15.1 20.0	(2) 16.8 16.1 17.5			
AHY-U					(550) 16.5 [1.32] 12.6 22.7	(95) 16.6 [1.02] 13.7 18.7	(67) 16.7 [0.89] 14.0 18.6	(193) 17.2 [1.14] 15.0 20.8	(92) 17.8 [1.64] 15.3 25.1	(1) 20.4		
SY-M					(1) 15.7	(1) 16.3	(1) 16.2					
SY-U					(6) 15.8 [0.95] 14.3 17.1		(1) 15.6					
ASY-F					(7) 16.2 [0.60] 15.4 17.3	(1) 17.2	(3) 15.5 15.0 16.1	(6) 16.8 [0.92] 15.4 18.3				
ASY-M					(2) 18.9 17.9 19.9	(1) 17.3	(1) 17.4	(3) 16.6 15.8 17.7				
ASY-U					(26) 15.9 [0.71] 14.9 18.2	(3) 17.2 16.6 18.1	(3) 16.6 16.3 16.9	(11) 17.0 [0.70] 15.9 18.1	(1) 17.3			
TY-F							(1) 17.1					
ATY-F					(5) 17.0 [2.21] 15.5 20.9	(1) 16.2	(4) 16.0 13.9 17.6	(12) 16.4 [1.08] 13.4 18.1				

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ATY-M					(18) 16.2 [0.80] 14.5 18.4	(2) 15.9 15.4 16.3		(7) 16.8 [0.38] 16.2 17.2				
ATY-U					(18) 16.3 [1.00] 15.1 18.6	(5) 16.4 [0.78] 15.4 17.6		(14) 17.4 [0.87] 16.2 19.5	(2) 15.3 12.0 18.6			
U-U								(3) 16.6 16.4 16.8				

Philadelphia Vireo

Vireo philadelphicus

n = 246

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(117) 12.0 [1.02] 9.4 15.3	(13) 12.6 [1.42] 11.2 15.4		
AHY-U					(79) 12.2 [1.14] 10.3 16.1				(16) 12.2 [0.90] 10.7 14.3	(6) 12.7 [0.94] 11.0 13.7		
U-U									(15) 11.8 [1.00] 10.4 13.7			

Warbling Vireo

Vireo gilvus

n = 20

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(5) 14.8 [0.99] 13.6 16.1			
AHY-U					(14) 13.6 [1.19] 11.4 17.0							
U-U								(1) 14.1				

Black-and-white Warbler

Mniotilta varia

n = 180

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(2) 9.5 9.4 9.6	(13) 10.1 [0.55] 9.3 11.1	(19) 10.6 [1.23] 8.3 14.0			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M							(2) 10.1 9.9 10.2	(17) 10.1 [0.77] 7.9 11.1	(26) 10.5 [0.83] 8.7 11.8			
HY-U							(1) 11.4	(5) 10.6 [0.75] 9.8 11.5	(2) 9.3 8.4 10.2			
AHY-F				(1) 9.9	(14) 10.8 [0.93] 9.0 12.7	(3) 10.3 9.7 11.2	(10) 10.9 [0.56] 10.2 12.2	(12) 10.3 [0.70] 9.3 11.1	(3) 10.3 10.0 10.9			
AHY-M				(5) 10.7 [0.88] 10.1 12.2	(9) 10.4 [0.95] 9.1 12.1		(2) 11.6 11.2 12.0	(2) 11.9 11.6 12.1	(5) 11.9 [2.80] 8.8 15.2			
SY-F					(1) 10.2							
SY-M					(1) 11.2							
U-F							(1) 10.3		(1) 9.3			
U-U								(18) 10.4 [0.69] 9.2 11.7	(5) 10.4 [0.68] 9.5 11.3			

Prothonotary Warbler

Protonotaria citrea

n = 1

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-M				(1) 12.9								

Worm-eating Warbler

Helmitheros vermivorus

n = 11

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(2) 12.6 12.2 12.9			
AHY-U				(2) 13.0 12.8 13.1	(6) 12.8 [0.67] 11.6 13.4							
U-U								(1) 12.2				

Golden-winged Warbler

Vermivora chrysoptera

n = 290

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(2) 8.7 7.1 10.3	(11) 8.3 [0.75] 7.0 9.8	(4) 8.8 8.1 9.4			
HY-M							(4) 9.8 9.6 10.4	(10) 8.8 [0.54] 8.0 9.9	(1) 9.0			
HY-U							(2) 8.2 7.9 8.5	(1) 7.7				
AHY-F					(64) 8.8 [0.88] 7.5 11.8	(7) 9.3 [0.98] 8.7 11.5	(2) 10.0 9.6 10.4	(4) 8.7 7.8 9.5	(1) 8.4			
AHY-M				(2) 9.4 8.9 9.8	(84) 8.7 [0.62] 7.2 11.2	(25) 8.8 [0.45] 7.7 9.4	(3) 9.2 8.8 9.7	(8) 8.6 [0.59] 8.0 9.5	(4) 8.6 7.6 9.8			
SY-F					(1) 8.1	(3) 9.8 8.5 11.3						
ASY-F						(1) 10.8						
ASY-M				(2) 8.8 8.5 9.0	(17) 8.8 [0.46] 7.9 10.0	(1) 8.7		(1) 9.3				
TY-F								(1) 8.9				
ATY-F					(3) 8.2 7.7 8.9		(2) 8.8 8.6 9.0		(1) 9.8			
ATY-M					(13) 8.6 [0.43] 7.7 9.4	(1) 9.1	(2) 9.4 9.1 9.6	(1) 8.9				
U-U								(1) 8.4				

"Brewster's" Warbler (hybrid)

Vermivora chrysoptera × *V. pinus*

n = 6

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(1) 7.7				

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U					(4) 8.6 7.8 9.2				(1) 8.8			
"Lawrence's" Warbler (hybrid) <i>Vermivora chrysoptera</i> × <i>V. pinus</i> n = 4												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M								(1) 7.8				
AHY-U				(1) 9.1	(1) 9.5							
TY-M					(1) 8.1							
Blue-winged Warbler <i>Vermivora pinus</i> n = 36												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M								(1) 7.4	(4) 9.2 8.1 9.8			
HY-U								(1) 8.1	(6) 8.2 [0.99] 7.3 9.9			
AHY-F					(5) 8.3 [0.41] 8.0 9.0	(1) 8.0			(2) 8.8 8.5 9.0			
AHY-M					(8) 8.2 [0.84] 7.2 10.0	(2) 8.0 7.9 8.0			(5) 9.3 [0.94] 8.7 11.0			
U-U								(1) 7.8				
Tennessee Warbler <i>Vermivora peregrina</i> n = 2523												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(9) 8.7 [0.65] 8.1 9.6			
HY-M									(8) 9.4 [0.48] 8.6 10.1			
HY-U								(36) 8.8 [0.62] 7.7 10.3	(1588) 9.0 [0.71] 7.3 15.3	(117) 9.7 [1.10] 7.6 14.8		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(164) 9.8 [1.09] 7.8 13.4				(4) 9.1 8.2 9.9			
AHY-M					(209) 10.2 [1.40] 7.3 18.4			(1) 9.9	(4) 9.2 8.7 9.8			
AHY-U					(100) 10.2 [1.33] 6.9 13.9		(1) 9.0	(9) 9.4 [0.76] 8.5 11.0	(92) 9.6 [1.02] 8.0 13.6	(3) 10.8 9.3 12.0		
U-U								(2) 8.4 7.9 8.8	(160) 9.1 [0.63] 7.7 10.9	(16) 10.7 [1.19] 8.4 12.6		

Orange-crowned Warbler

Vermivora celata

n = 108

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(4) 8.4 7.9 8.7	(63) 9.6 [0.81] 7.9 11.7	(2) 10.9 9.7 12.1	
AHY-F					(1) 8.8							
AHY-M										(1) 10.5		
AHY-U				(1) 9.8	(12) 9.4 [0.47] 8.6 9.9					(20) 9.2 [0.70] 8.1 10.9	(1) 9.4	
U-U										(3) 9.4 9.0 10.0		

Nashville Warbler

Vermivora ruficapilla

n = 920

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(2) 8.0 7.9 8.0	(136) 8.5 [0.86] 7.1 11.7	(43) 8.8 [0.76] 7.3 10.4		
HY-M								(1) 7.1	(87) 8.7 [0.79] 7.5 10.6	(22) 9.3 [0.95] 7.7 12.2	(4) 8.2 7.2 9.0	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(2) 8.4 8.2 8.5	(35) 8.6 [0.84] 7.3 10.6	(6) 9.1 [0.96] 7.5 10.1		
AHY-F				(4) 7.8 6.8 8.3	(158) 8.5 [0.72] 6.7 11.1			(1) 9.5	(57) 8.5 [0.72] 7.0 10.2	(37) 8.9 [0.72] 7.5 10.2		
AHY-M				(11) 8.2 [0.74] 7.2 9.6	(135) 9.0 [0.98] 7.2 13.9				(29) 9.0 [1.01] 7.4 12.2	(20) 8.9 [0.89] 7.0 11.2		
AHY-U				(1) 8.7	(60) 8.6 [0.71] 7.1 10.2				(12) 9.0 [0.97] 7.9 10.5	(1) 8.0		
U-M									(1) 8.3	(2) 8.4 7.9 8.8		
U-U								(5) 7.9 [0.85] 7.4 9.4	(39) 8.6 [0.70] 7.4 9.9	(9) 9.1 [0.97] 7.3 10.2		

Northern Parula

Parula americana

n = 23

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M									(3) 8.3 7.2 10.0			
HY-U							(1) 7.3	(1) 7.7	(3) 7.4 7.0 7.7			
AHY-F					(3) 7.7 7.1 8.5	(1) 7.4				(1) 7.2		
AHY-M					(8) 8.1 [0.87] 7.0 9.6			(1) 8.4				
U-U									(1) 9.3			

Yellow Warbler											
<i>Dendroica petechia</i>											
n = 376											
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov. Dec.
HY-F								(1) 12.6			
HY-U							(15) 9.3 [0.80] 8.0 10.7	(11) 10.9 [1.60] 9.2 13.8	(10) 10.1 [1.02] 8.4 11.5	(1) 10.0	
AHY-F				(3) 9.5 9.1 10.0	(110) 9.1 [0.74] 7.4 12.0	(1) 9.2	(5) 9.4 [0.63] 8.8 10.4	(4) 10.5 10.0 11.2	(1) 16.0		
AHY-M				(7) 10.2 [1.09] 9.3 12.5	(131) 9.8 [0.79] 7.9 12.4	(15) 9.3 [0.60] 8.1 10.2	(6) 10.0 [0.83] 9.0 10.9	(2) 11.8 10.8 12.8	(3) 10.6 10.1 11.0		
AHY-U								(2) 11.4 10.9 11.8			
ASY-F					(3) 8.9 8.7 9.0						
ASY-M				(1) 10.3	(11) 9.5 [0.52] 8.6 10.3	(1) 9.8					
ATY-F				(1) 9.8	(9) 9.4 [0.75] 8.5 10.7	(1) 9.2		(1) 11.0			
ATY-M				(1) 10.4	(8) 9.9 [0.46] 8.6 12.0						
U-U							(1) 8.9	(8) 11.0 [1.55] 8.7 13.5	(2) 9.2 9.2		
Magnolia Warbler											
<i>Dendroica magnolia</i>											
n = 2561											
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov. Dec.
HY-U								(85) 8.1 [0.54] 6.0 9.7	(1214) 8.2 [0.70] 6.6 12.9	(50) 8.8 [1.06] 6.9 11.5	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F				(1) 7.6	(238) 8.5 [0.81] 6.6 12.6	(1) 8.3		(2) 8.0 7.5 8.4	(165) 8.4 [0.76] 6.7 12.4	(23) 9.5 [1.30] 7.7 11.8		
AHY-M					(390) 8.9 [0.81] 7.0 12.9	(2) 9.0 8.6 9.4		(2) 9.0 7.9 10.1	(97) 8.6 [0.62] 7.2 9.9	(16) 9.6 [1.06] 8.3 12.7		
AHY-U					(30) 8.2 [0.82] 6.6 10.0			(3) 7.9 7.5 8.2	(42) 8.8 [0.83] 7.1 11.2	(1) 9.4		
SY-M					(11) 8.5 [0.91] 7.4 10.5							
SY-U									(1) 8.3			
ASY-M					(12) 8.9 [0.91] 7.7 10.6							
ATY-M									(1) 9.2			
U-U								(14) 8.1 [0.47] 7.3 8.8	(155) 8.3 [0.64] 6.9 10.9	(5) 9.1 [0.87] 8.3 10.5		
Cape May Warbler					<i>Dendroica tigrina</i>					n = 798		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(2) 9.3 8.9 9.7	(280) 10.0 [0.98] 8.2 16.5	(13) 9.9 [2.01] 8.9 15.1		
HY-M								(1) 10.4	(280) 10.1 [0.89] 8.5 16.1	(17) 11.3 [2.29] 8.8 17.3		
HY-U								(1) 9.7	(51) 10.0 [0.92] 8.1 13.1	(7) 11.7 [2.10] 8.9 13.9		
AHY-F					(10) 11.1 [1.34] 9.7 14.0			(1) 10.5	(27) 10.4 [0.85] 9.3 13.4	(2) 12.9 10.5 15.3		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-M					(11) 11.2 [1.06] 9.9 13.1			(6) 11.0 [0.91] 10.0 12.4	(42) 11.2 [1.79] 9.3 17.3	(2) 13.2 11.1 15.2		
AHY-U								(1) 9.4	(33) 10.6 [1.53] 8.8 15.3	(4) 11.0 8.3 9.6		
U-F									(1) 9.6			
U-U									(5) 10.5 [0.73] 9.5 11.4	(1) 13.5		

Black-throated Blue Warbler

Dendroica caerulescens

n = 129

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(3) 8.7 8.5 8.8 10.2	(27) 9.2 [0.51] 8.2 12.7	(7) 10.5 [1.39] 8.8 12.7		
HY-M								(1) 10.0	(31) 9.8 [0.67] 8.7 11.8	(3) 10.1 9.5 10.8		
HY-U									(1) 9.3			
AHY-F					(24) 9.6 [0.84] 8.1 11.7			(1) 9.1	(2) 11.0 9.9 12.1			
AHY-M					(9) 9.9 [0.76] 8.8 11.0			(1) 9.4	(4) 9.4 8.7 10.0	(2) 10.3 10.6	(1) 9.9	
U-F									(10) 9.0 [0.43] 8.5 10.0			
U-M									(1) 10.5	(1) 10.2		

Yellow-rumped Warbler (Myrtle Warbler)

Dendroica coronata

n = 2095

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(15) 11.0 [0.80] 9.7 12.4	(323) 12.0 [1.07] 9.6 16.5	(7) 12.4 [0.92] 11.4 13.6	

1978

CLENCH AND LEBERMAN—PENNSYLVANIA BIRD WEIGHTS

47

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M									(3) 11.6 9.7 12.8	(193) 12.8 [1.17] 10.6 19.7	(20) 13.5 [1.12] 11.6 15.7	
HY-U									(28) 11.4 [0.69] 10.6 13.6	(783) 12.5 [1.25] 9.5 16.6	(24) 13.5 [1.24] 10.9 15.6	
AHY-F				(5) 12.3 [1.72] 10.3 14.7	(60) 11.8 [0.95] 10.1 14.5				(5) 11.5 [0.43] 10.9 12.0	(213) 12.3 [1.07] 9.9 15.3	(5) 12.9 [1.41] 11.5 14.5	
AHY-M				(18) 13.4 [1.30] 11.8 16.6	(45) 12.4 [0.90] 10.8 15.1					(152) 13.1 [1.20] 10.8 16.7	(1) 14.3	
AHY-U				(1) 11.0	(9) 12.6 [1.03] 11.0 14.3				(1) 12.1	(29) 13.0 [1.10] 10.8 14.7	(1) 13.4	
SY-M					(5) 11.3 [0.69] 10.6 12.2							
ASY-M					(9) 12.2 [0.99] 10.8 13.5							
U-F										(1) 12.3	(1) 14.5	
U-M											(1) 12.9	
U-U									(6) 11.0 [0.87] 10.3 12.6	(121) 12.0 [1.03] 9.7 15.6	(10) 13.3 [0.95] 11.6 14.8	

Black-throated Green Warbler

Dendroica virens

n = 563

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F									(4) 8.2 7.8 8.9			
HY-M									(18) 9.0 [0.51] 8.0 9.9			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(2) 8.7 8.2 9.1	(22) 8.3 [0.44] 7.7 9.5	(357) 8.6 [0.64] 7.1 11.2	(38) 9.0 [0.72] 7.5 11.2		
AHY-F					(5) 8.8 [0.58] 8.1 9.5		(1) 9.3		(10) 8.9 [0.76] 7.7 10.1	(1) 9.9		
AHY-M				(2) 8.9 8.7 9.0	(11) 10.0 [1.66] 8.6 14.4		(1) 8.6	(2) 8.2 7.9 8.5	(25) 9.0 [0.74] 8.0 11.4	(2) 9.8 9.2 10.3		
AHY-U								(2) 8.1 7.9 8.2	(3) 9.0 9.0 9.0			
SY-F							(1) 7.9					
U-F									(1) 9.2			
U-M									(6) 8.4 [0.24] 8.1 8.8	(1) 9.0		
U-U								(5) 8.5 [0.30] 8.1 8.8	(40) 8.5 [0.53] 7.4 9.8	(3) 9.1 8.6 9.0		
Cerulean Warbler						<i>Dendroica cerulea</i>					n = 36	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U							(12) 9.0 [0.73] 8.0 10.2	(4) 8.8 8.2 9.5	(2) 8.7 8.4 9.0			
AHY-F					(1) 9.1		(1) 9.2	(2) 9.0 8.8 9.1				
AHY-M					(2) 9.4 9.1 9.7	(3) 9.5 9.0 10.0	(4) 9.5 9.3 9.7	(1) 9.2				
AHY-U								(1) 9.0				
U-U								(3) 8.7 8.1 9.2				

Blackburnian Warbler

Dendroica fusca

n = 90

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(6) 9.1 [0.63] 8.3 9.8	(20) 9.0 [0.65] 8.1 10.5			
HY-M								(4) 9.6 9.2 10.3	(30) 9.7 [0.91] 8.0 12.7			
HY-U								(7) 9.1 [0.55] 8.3 10.0	(7) 9.2 [0.86] 7.7 10.0			
AHY-F					(2) 10.2 10.1 10.2	(1) 9.3			(1) 10.0			
AHY-M					(3) 10.7 10.0 11.4			(1) 9.6	(2) 10.4 9.8 10.9			
AHY-U									(1) 9.4			
U-U								(3) 8.9 8.6 9.3	(2) 9.2 9.2 9.3			

Chestnut-sided Warbler

Dendroica pensylvanica

n = 375

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M							(1) 9.4	(3) 9.7 9.0 11.0	(26) 9.5 [0.74] 8.0 11.6			
HY-U								(59) 9.1 [0.58] 8.2 10.4	(147) 9.4 [0.73] 7.8 11.6	(2) 9.6 8.6 10.6		
AHY-F					(26) 9.5 [0.72] 7.5 10.9	(2) 9.7 9.0 10.3	(1) 9.4	(2) 9.1 8.7 9.5	(14) 9.3 [0.70] 7.7 10.5	(1) 9.1		
AHY-M					(45) 9.9 [0.95] 8.1 13.1	(1) 10.1	(1) 10.0	(2) 9.9 9.8 10.0	(17) 9.7 [0.59] 8.9 11.2			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U					(3) 9.6 8.5 10.4			(6) 9.7 [0.87] 8.4 10.7	(4) 10.2 9.0 12.1	(1) 9.2		

U-U								(6) 9.1 [0.53] 8.7 10.1	(5) 10.0 [0.95] 9.0 11.6			
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Bay-breasted Warbler

Dendroica castanea

n = 279

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M									(3) 12.3 11.1 13.7			
HY-U								(2) 11.5 11.3 12.0	(223) 11.6 [0.76] 9.7 14.0	(2) 11.9 11.5 12.3		
AHY-F					(6) 11.9 [1.02] 10.7 13.6				(8) 12.0 [0.88] 10.8 13.1			
AHY-M					(11) 13.4 [1.17] 12.0 15.1				(4) 12.0 11.6 12.3	(1) 13.7		
AHY-U									(15) 11.9 [0.86] 10.2 13.2			
U-U									(3) 12.2 10.5 12.8	(1) 14.1		

Blackpoll Warbler

Dendroica striata

n = 484

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(192) 11.8 [0.86] 9.8 14.5	(83) 13.5 [2.06] 10.4 20.8		
AHY-F					(6) 12.3 [0.80] 11.2 13.6	(2) 14.0 11.5 16.4			(6) 12.3 [2.38] 9.8 16.8			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-M					(22) 13.0 [1.14] 10.8 15.9				(2) 13.3 12.3 14.2			
AHY-U									(53) 12.2 [1.44] 9.7 19.0	(29) 15.5 [2.91] 12.1 21.6		
U-U								(1) 11.6	(70) 12.2 [1.17] 10.7 18.1	(18) 15.1 [2.96] 12.0 20.9		
Pine Warbler					<i>Dendroica pinus</i>							n = 3
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(1) 11.7	(1) 11.1	(1) 14.2		
Kirtland's Warbler					<i>Dendroica kirtlandii</i>							n = 3
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(2) 14.5 14.0 14.9	(1) 15.8		
(n.b., all 3 weights are from the same individual)												
Prairie Warbler					<i>Dendroica discolor</i>							n = 83
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(2) 6.7 6.5 6.8	(2) 7.7 7.2 8.2			
HY-M								(1) 7.0	(3) 7.6 6.9 8.2	(1) 8.3		
HY-U							(1) 7.8	(2) 6.8 6.6 7.0				
AHY-F				(2) 6.9 6.8 7.0	(32) 7.0 [0.48] 6.2 8.1	(1) 8.0	(2) 7.1 7.1	(2) 7.2 6.9 7.5	(1) 7.8			
AHY-M				(6) 7.2 [0.50] 6.7 7.9	(17) 7.2 [0.42] 6.2 7.8	(3) 7.2 6.6 8.0		(1) 8.7	(1) 8.7			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U				(2) 7.2 7.0 7.4	(1) 6.7							
<i>Palm Warbler</i>												
<i>Dendroica palmarum</i>												
											n = 568	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(233) 10.2 [0.81] 7.9 12.2	(156) 10.6 [0.97] 8.3 13.2	(3) 11.5 10.2 13.0	
AHY-M				(2) 10.3 9.8 10.8						(2) 10.9 10.3 11.5		
AHY-U				(6) 10.2 [0.38] 9.6 10.7	(5) 10.2 [0.70] 9.4 11.1				(2) 10.5 10.4 10.6	(30) 10.7 [0.92] 9.3 12.9		
U-U									(91) 10.0 [0.92] 7.0 12.3	(38) 10.5 [0.72] 9.2 11.8		
<i>Ovenbird</i>												
<i>Seiurus aurocapillus</i>												
											n = 449	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M								(2) 20.0 19.6 20.3				
HY-U							(9) 19.1 [1.40] 17.3 21.5	(48) 18.9 [1.60] 17.0 26.3	(193) 19.4 [1.98] 16.4 28.2	(16) 20.2 [3.12] 17.5 28.3		
AHY-F						(5) 19.6 [1.53] 18.1 21.7						
AHY-M					(3) 18.6 18.1 19.3	(9) 18.8 [0.85] 17.4 20.3	(1) 20.5					
AHY-U				(2) 18.0 17.7 18.2	(34) 18.8 [1.87] 15.6 23.4		(1) 19.4	(10) 18.9 [1.34] 16.5 20.5	(29) 19.0 [1.40] 15.7 22.0	(4) 22.4 20.3 26.2		
SY-M						(1) 18.3						

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-U								(2) 19.1 19.0 19.1	(1) 28.8			
U-U							(1) 18.9	(12) 18.6 [1.42] 16.9 21.0	(62) 20.0 [2.21] 14.0 26.5	(4) 20.3 19.4 20.9		

Northern Waterthrush

Seiurus noveboracensis

n = 458

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(34) 17.9 [1.63] 15.1 22.0	(109) 18.1 [1.81] 14.3 23.9	(26) 18.9 [2.50] 15.3 23.1		
AHY-U				(16) 16.7 [1.67] 13.8 20.5	(169) 17.6 [1.67] 14.2 24.4			(32) 18.6 [1.31] 16.4 21.6	(26) 18.4 [1.66] 15.4 23.2	(4) 19.0 17.8 20.2		
U-U								(10) 17.9 [0.94] 16.5 19.5	(31) 18.1 [1.90] 13.9 23.3	(1) 16.2		

Louisiana Waterthrush

Seiurus motacilla

n = 103

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U						(2) 20.9 20.6 21.1	(12) 20.0 [2.03] 14.5 22.1	(9) 20.2 [1.71] 18.1 24.0	(1) 17.2			
AHY-F					(5) 21.5 [2.83] 18.2 26.0	(2) 20.2 20.1 20.2	(2) 20.4 19.4 21.4					
AHY-M					(15) 19.7 [1.31] 17.4 22.1	(1) 22.7						
AHY-U				(7) 19.0 [0.91] 17.3 20.1	(29) 19.6 [1.23] 17.0 22.4		(2) 22.5 21.7 23.2					
ASY-F					(1) 21.3							
ASY-M					(7) 19.3 [0.86] 18.3 20.6							

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-U					(3) 18.5 18.3 18.7			(1) 18.7				
ATY-M				(2) 20.7 20.3 21.1								
U-U							(2) 19.7 19.3 20.1					
Kentucky Warbler <i>Oporornis formosus</i> n = 206												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(3) 13.4 13.3 13.5	(4) 13.4 12.3 14.3			
HY-M							(2) 14.4 13.8 14.9	(14) 14.1 [1.08] 12.3 16.7	(5) 14.1 [0.50] 13.4 14.7			
HY-U							(4) 14.0 12.9 15.2	(15) 14.2 [0.86] 13.0 16.7	(3) 14.0 12.1 15.9			
AHY-F					(19) 13.1 [1.18] 11.4 16.5	(4) 14.0 12.8 15.8	(7) 13.6 [0.92] 12.6 15.3	(8) 15.0 [0.65] 14.1 16.1	(1) 14.7			
AHY-M				(3) 14.2 13.9 14.5	(49) 14.0 [0.67] 12.0 15.5	(14) 14.1 [0.71] 12.9 15.5	(3) 14.8 13.8 16.3	(13) 14.9 [1.36] 13.8 18.3	(2) 18.5 16.3 20.6			
AHY-U					(1) 12.4		(1) 13.8	(2) 14.9 13.3 16.4				
ASY-F					(1) 13.3		(1) 12.7	(1) 13.2	(1) 14.1			
ASY-M				(1) 12.2				(1) 17.9	(3) 14.6 14.3 15.0			
ASY-U								(1) 14.5				
ATY-M					(3) 13.7 13.2 14.2			(1) 15.5	(1) 15.4			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-M									(2) 14.0 13.4 14.6			
U-U								(11) 13.5 [0.57] 12.7 14.4	(1) 14.8			
<i>Connecticut Warbler</i>												
<i>Oporornis agilis</i>												
n = 217												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(4) 13.8 13.2 14.5	(107) 14.0 [1.32] 11.5 19.7	(12) 14.9 [2.11] 12.3 19.7		
AHY-F					(4) 13.3 10.4 19.1			(1) 12.7	(17) 14.4 [2.14] 12.4 21.2	(3) 13.7 12.1 15.5		
AHY-M					(4) 16.5 16.2 16.8				(28) 14.9 [2.34] 10.7 20.2	(4) 15.9 12.3 22.0		
AHY-U									(8) 14.6 [3.31] 12.1 22.2			
U-U									(23) 14.3 [1.93] 12.5 21.0	(2) 17.7 13.6 21.7		
<i>Mourning Warbler</i>												
<i>Oporornis philadelphia</i>												
n = 319												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 11.3	(2) 13.8 12.5 15.0			
HY-M									(3) 11.5 11.1 11.8	(2) 15.2 13.8 16.5		
HY-U								(21) 11.9 [1.00] 10.6 14.2	(50) 12.5 [1.10] 10.4 15.0	(7) 12.9 [1.20] 11.1 14.5		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(45) 11.9 [1.02] 10.0 14.7	(9) 12.5 [1.00] 11.0 14.0	(1) 12.2 [0.56] 11.8 13.3	(5) 12.5 [0.56] 11.8 13.3	(24) 12.0 [1.00] 10.5 13.8	(5) 12.2 [1.70] 10.0 14.0		
AHY-M					(89) 12.9 [1.02] 10.8 15.6	(5) 13.2 [0.75] 12.5 14.3		(10) 12.6 [1.36] 9.6 13.9	(30) 13.1 [1.54] 10.3 17.9	(5) 13.4 [1.10] 12.2 14.6		
AHY-U					(4) 12.3 11.0 14.0							
U-M									(1) 13.2			
Common Yellowthroat <i>Geothlypis trichas</i> n = 3712												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(3) 9.2 8.8 9.5	(80) 9.3 [0.62] 8.0 11.0	(488) 9.7 [1.03] 7.9 14.3	(119) 10.5 [1.23] 8.2 13.7	(2) 10.6 10.5 10.7	
HY-M							(11) 9.4 [0.89] 8.3 11.4	(112) 9.9 [0.68] 8.7 12.5	(695) 10.2 [1.08] 8.0 13.7	(156) 11.0 [1.33] 8.7 14.7	(1) 10.8	
HY-U							(66) 9.1 [0.52] 8.1 10.7	(137) 9.7 [0.75] 8.1 12.1	(61) 10.0 [1.10] 7.4 12.7	(10) 10.8 [1.57] 8.6 13.5		
AHY-F					(194) 9.5 [1.02] 7.6 13.0	(14) 9.9 [0.76] 8.9 11.5	(25) 9.6 [0.67] 8.1 10.7	(34) 9.6 [0.70] 8.1 11.7	(178) 10.0 [1.11] 7.8 15.3	(50) 11.0 [1.06] 8.6 12.8	(1) 9.2	
AHY-M				(17) 9.4 [0.44] 8.6 10.4	(325) 10.1 [0.99] 7.6 13.3	(25) 9.8 [0.55] 8.9 10.6	(27) 9.6 [0.36] 9.1 10.4	(20) 10.3 [0.70] 9.1 11.7	(276) 10.8 [1.17] 8.6 15.2	(33) 12.1 [1.63] 9.5 15.5		
AHY-U					(2) 9.9 9.0 10.8				(5) 10.0 [0.63] 9.1 10.6			
SY-F					(2) 8.7 8.6 8.7		(4) 9.2 8.9 9.9	(2) 10.7 10.2 11.1	(2) 10.1 9.7 10.4			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
SY-M					(39) 9.7 [0.64] 8.4 11.7	(10) 9.6 [0.62] 8.6 10.4	(3) 9.7 9.0 10.3	(2) 9.4 8.8 9.9	(7) 10.1 [0.50] 9.1 10.6			
ASY-F					(16) 9.4 [0.95] 8.1 11.6	(2) 12.3 11.6 12.9	(2) 10.7 10.6 10.7	(3) 9.5 9.2 9.7	(5) 9.4 [0.45] 8.7 9.8	(2) 9.6 8.5 10.6		
ASY-M					(80) 10.3 [1.09] 8.6 13.4	(6) 9.9 [0.50] 9.2 10.4	(1) 8.8	(3) 9.8 9.2 10.7	(3) 10.3 9.6 11.0	(2) 10.7 10.2 11.2		
TY-F					(4) 8.9 7.6 10.7				(2) 9.5 9.0 9.9			
TY-M					(15) 9.6 [0.57] 8.6 10.5		(1) 9.7	(2) 9.7 9.7 9.7	(2) 10.7 10.5 10.8	(1) 12.3		
ATY-F					(9) 8.8 [0.47] 8.1 9.6	(1) 10.6	(2) 8.6 7.7 9.5	(2) 9.0 8.9 9.0	(6) 9.5 [0.93] 8.3 10.9	(1) 10.3		
ATY-M				(1) 10.7	(39) 9.4 [0.56] 8.5 11.1	(7) 9.7 [0.63] 8.9 10.9	(1) 9.6	(6) 10.0 [0.33] 9.6 10.4	(2) 10.1 9.5 10.7			
U-F								(4) 8.8 8.3 9.5	(71) 10.3 [1.02] 8.0 12.6	(5) 10.4 [0.98] 9.0 11.7	(1) 10.1	
U-M							(1) 9.2	(7) 10.1 [0.16] 9.8 10.3	(1) 12.6			
U-U							(15) 9.4 [0.57] 8.4 10.6	(126) 9.9 [0.97] 8.3 12.8	(14) 10.4 [1.40] 9.1 13.7			

Yellow-breasted Chat

Icteria virens

n = 564

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(7) 28.1 [1.87] 25.6 30.6	(6) 27.3 [2.79] 23.2 30.1			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M								(2) 24.2 23.0 25.4	(3) 25.1 22.9 26.6			
HY-U							(12) 24.4 [1.67] 22.2 27.8	(43) 26.0 [2.62] 22.4 34.1	(36) 28.3 [2.25] 24.3 32.8	(5) 29.5 [2.11] 26.7 31.8		
AHY-F				(1) 25.5	(101) 24.0 [2.24] 20.2 32.0	(11) 26.1 [1.44] 24.6 29.5	(21) 25.6 [1.57] 23.5 29.3	(15) 27.4 [2.50] 24.0 33.6	(10) 29.4 [2.29] 26.3 33.1	(1) 33.8		
AHY-M				(2) 25.7 25.6 25.7	(166) 25.0 [1.89] 20.3 30.4	(22) 25.2 [1.44] 22.4 28.2	(12) 26.0 [1.24] 24.5 28.3	(11) 27.8 [2.24] 23.9 30.0	(9) 28.3 [1.96] 25.4 31.7			
AHY-U				(1) 22.8	(9) 24.1 [1.23] 21.5 25.8		(5) 26.2 [2.53] 23.5 29.2	(7) 27.9 [2.47] 24.2 31.7	(1) 28.8	(1) 32.5		
ASY-F					(4) 24.7 23.4 26.1			(1) 24.8				
ASY-M					(4) 25.0 24.2 27.1	(1) 23.6		(2) 29.6 29.5 29.6	(1) 29.5			
TY-M					(1) 25.6							
ATY-F					(2) 24.2 23.5 24.8							
ATY-M					(14) 26.1 [2.12] 22.0 29.3			(1) 26.7	(2) 27.0 23.2 30.8			
ATY-U					(1) 24.0							
U-F									(5) 27.0 [1.12] 25.5 28.5	(1) 27.7		
U-U								(2) 27.9 27.4 28.3	(1) 30.4	(1) 25.6		

Hooded Warbler

Wilsonia citrina

n = 370

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(36) 9.8 [0.54] 8.8 11.2	(64) 9.8 [0.69] 8.1 11.6	(6) 11.6 [1.85] 10.0 14.9		
HY-M								(11) 10.8 [0.63] 9.9 12.0	(43) 10.3 [0.65] 7.4 11.8	(5) 10.9 [0.60] 10.3 11.8		
AHY-F					(36) 9.8 [0.55] 8.6 11.2	(5) 11.0 [0.67] 10.5 12.2	(2) 11.0 10.5 11.4	(2) 10.6 10.1 11.1	(7) 10.2 [0.43] 9.3 10.5	(1) 11.2		
AHY-M					(18) 10.8 [0.62] 9.4 11.8	(3) 10.7 10.0 11.3 11.7	(3) 11.3 10.8 11.7	(4) 10.0 9.7 10.4	(2) 11.2 9.9 12.4			
ASY-M					(1) 11.0							
ATY-F					(1) 9.7			(1) 12.1	(1) 12.5			
ATY-U									(1) 10.9			
U-F								(28) 10.0 [0.76] 8.7 12.3	(31) 10.2 [0.69] 8.2 11.8			
U-M								(25) 10.5 [0.84] 8.1 12.3	(30) 11.0 [0.82] 9.9 12.9	(3) 11.7 10.0 13.9		

Wilson's Warbler

Wilsonia pusilla

n = 746

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(20) 7.5 [0.64] 6.5 9.3	(68) 7.7 [0.78] 6.0 11.9	(1) 8.8		
HY-M								(17) 7.8 [0.66] 6.5 9.0	(74) 8.0 [0.73] 6.7 10.9	(3) 7.6 7.3 8.3		
HY-U									(7) 7.8 [0.45] 7.3 8.7	(1) 6.8		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(44) 7.4 [0.55] 6.3 8.8	(1) 9.1		(1) 7.5	(25) 7.9 [0.84] 6.5 9.5			
AHY-M					(297) 7.6 [0.54] 6.4 9.3	(3) 8.1 7.3 9.5		(8) 7.5 [0.54] 6.4 8.1	(112) 8.0 [0.72] 6.7 10.5	(3) 8.5 7.1 10.0		
AHY-U					(26) 7.3 [0.47] 6.5 8.4			(2) 7.8 6.9 8.7	(10) 8.0 [1.01] 6.6 9.1			
U-F									(6) 7.6 [0.69] 7.1 8.9			
U-M								(1) 7.7	(1) 7.6			
U-U								(1) 7.0	(14) 7.4 [0.57] 6.6 8.2			

Canada Warbler

Wilsonia canadensis

n = 825

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(5) 10.0 [0.86] 8.8 11.2	(1) 10.3			
HY-M								(1) 11.1	(1) 9.2			
HY-U							(1) 9.5	(101) 10.2 [0.84] 8.7 12.7	(90) 10.3 [0.83] 8.4 14.7			
AHY-F				(1) 10.6	(226) 10.2 [0.73] 8.1 12.6	(4) 10.9 10.1 11.8	(1) 9.3	(15) 10.6 [0.63] 9.5 11.6	(16) 10.2 [0.61] 9.1 10.8			
AHY-M					(289) 10.6 [0.80] 8.7 13.5			(7) 11.2 [0.50] 10.5 11.7	(13) 10.6 [0.79] 9.5 11.9			
AHY-U					(5) 9.5 [0.36] 9.2 10.0			(5) 10.0 [0.70] 9.2 11.1	(1) 10.2			

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug. (34) 10.1 [0.83] 8.6 11.9	Sept. (7) 10.2 [0.74] 9.5 11.5	Oct. (1) 11.0	Nov.	Dec.
American Redstart											n = 919	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(5) 8.0 [0.33] 7.6 8.5	(42) 7.8 [0.37] 7.2 9.2	(203) 8.0 [0.67] 6.5 10.3	(1) 7.5		
HY-M							(5) 8.4 [0.46] 7.8 9.1	(26) 8.1 [0.64] 7.0 9.5	(138) 8.1 [0.67] 6.7 10.1	(6) 9.1 [1.72] 7.5 12.2		
HY-U						(2) 9.7 9.5 9.8	(15) 8.7 [0.61] 7.3 9.6	(17) 8.2 [0.50] 7.3 9.0	(78) 7.8 [0.66] 6.4 10.0	(1) 7.7		
AHY-F					(90) 8.0 [0.67] 6.7 10.1	(6) 8.3 [0.50] 7.8 9.2	(12) 8.2 [0.46] 7.5 9.1	(18) 8.4 [0.81] 7.2 10.7	(24) 8.3 [0.93] 7.4 11.2	(2) 8.3 8.2 8.3		
AHY-M					(15) 8.3 [0.58] 7.0 9.1	(2) 8.5 8.1 8.8	(2) 8.6 8.6 8.7	(9) 9.1 [1.26] 7.7 12.0	(27) 8.2 [0.78] 7.2 11.0	(1) 11.6		
AHY-U					(3) 7.7 7.3 8.2			(2) 9.2 9.0 9.4				
SY-F					(1) 7.8							
SY-M					(37) 8.4 [0.57] 7.2 9.7	(7) 8.4 [0.28] 8.0 8.7	(1) 9.1					
ASY-F					(5) 8.1 [1.20] 7.2 10.2	(2) 8.6 7.5 9.6	(1) 10.4					
ASY-M				(1) 8.2	(22) 8.4 [0.78] 7.3 9.9	(3) 8.7 8.2 9.0	(2) 9.3 8.9 9.7	(2) 8.9 8.6 9.2	(7) 8.2 [0.34] 7.8 8.7			
ATY-F					(3) 7.5 7.2 8.1							

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ATY-M					(3) 8.8 8.1 9.2		(1) 9.4	(1) 9.6				
U-F							(3) 8.3 7.6 9.2	(1) 8.1	(2) 7.3 7.1 7.4			
U-U							(1) 8.0	(18) 7.8 [0.54] 6.8 8.6	(41) 7.7 [0.44] 6.8 8.7	(2) 10.1 8.6 11.6		
House Sparrow	<i>Passer domesticus</i>										n = 1541	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F					(1) 24.4	(3) 23.3 22.2 24.1	(18) 26.2 [1.64] 21.9 29.1	(6) 27.2 [1.36] 26.1 29.3	(38) 27.3 [1.70] 23.5 30.7	(54) 27.9 [1.61] 24.6 33.5	(76) 27.2 [1.94] 21.0 31.4	(9) 27.5 [1.23] 25.4 29.0
HY-M					(5) 22.6 [2.61] 20.3 26.5	(5) 26.6 [2.26] 25.0 30.5	(19) 28.2 [1.84] 25.2 31.9	(2) 25.2 24.3 26.0	(19) 27.7 [1.74] 24.3 30.6	(63) 28.3 [1.58] 24.1 32.7	(102) 28.2 [1.96] 24.3 33.6	(6) 27.8 [1.53] 25.4 29.9
HY-U					(11) 26.0 [1.85] 23.1 29.0	(44) 25.8 [1.86] 22.0 29.8	(46) 26.4 [1.98] 21.6 29.5	(1) 24.1		(3) 26.9 26.7 27.0		
AHY-F	(41) 26.3 [1.52] 22.2 29.3	(25) 27.0 [1.48] 23.4 29.4	(94) 26.9 [1.65] 20.1 29.7	(81) 28.2 [2.21] 22.7 33.7	(19) 28.2 [2.34] 24.6 32.5	(2) 28.9 28.4 29.3			(2) 27.1 23.2 31.0	(6) 28.4 [1.12] 26.5 29.3	(6) 26.4 [1.95] 23.6 29.5	(2) 28.2 27.9 28.4
AHY-M	(44) 27.9 [1.83] 23.1 32.0	(37) 28.0 [1.55] 24.0 30.6	(109) 28.0 [1.48] 23.7 31.2	(64) 28.6 [2.00] 23.2 34.0	(14) 27.6 [2.69] 20.0 30.9	(6) 28.0 [0.80] 27.0 29.1	(3) 28.7 26.3 33.3	(1) 26.8	(1) 26.0	(3) 27.9 23.7 32.5	(14) 27.8 [1.72] 24.1 30.8	(3) 26.6 25.3 28.3
AHY-U				(1) 27.2								
SY-F	(7) 26.2 [1.21] 24.8 27.7	(6) 28.0 [0.67] 26.9 28.8	(19) 27.1 [2.07] 21.2 30.6	(7) 28.5 [2.02] 26.2 32.5	(9) 27.8 [1.96] 25.3 31.3	(4) 27.6 25.5 28.3				(2) 23.9 20.4 27.4	(1) 24.4	
SY-M	(16) 27.8 [1.14] 25.6 29.4	(4) 26.6 24.8 29.4	(30) 28.1 [1.46] 24.6 31.6	(13) 27.4 [1.44] 25.1 30.0	(5) 28.0 [0.85] 27.3 29.4	(1) 26.5				(1) 28.1		
ASY-F		(3) 27.0 26.0 28.2	(9) 26.8 [2.71] 22.7 30.8	(6) 28.3 [0.76] 27.2 28.9	(4) 28.6 25.4 34.5			(1) 27.2			(4) 27.2 25.1 28.4	(1) 27.8

1978

CLENCH AND LEBERMAN—PENNSYLVANIA BIRD WEIGHTS

63

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-M	(3) 26.3 25.3 27.6	(4) 27.7 25.6 29.2	(19) 27.7 [1.28] 25.9 30.2	(14) 27.6 [1.01] 26.3 29.7	(10) 27.2 [2.15] 24.5 31.2	(1) 27.0						(1) 28.7
TY-F	(1) 28.0		(6) 27.2 [1.42] 25.6 29.2	(3) 29.6 27.4 32.0	(1) 31.1							
TY-M	(1) 28.9	(1) 25.4	(7) 27.7 [1.43] 25.0 29.4									
ATY-F	(2) 26.6 26.2 26.9	(2) 27.2 25.9 28.4	(5) 27.6 [1.38] 25.6 29.0	(4) 28.4 25.9 31.2	(2) 26.4 25.1 27.6	(1) 27.5					(4) 29.0 26.8 30.4	
ATY-M	(2) 26.7 26.4 27.0	(2) 27.2 27.0 27.3	(11) 28.2 [1.15] 26.4 30.0	(3) 27.6 25.5 30.2	(5) 29.7 [0.96] 28.3 30.8	(3) 28.5 27.5 29.4				(1) 29.1	(1) 27.0	(1) 27.5
U-F									(1) 32.0	(10) 27.6 [1.53] 25.2 30.0	(57) 27.2 [1.80] 22.6 30.3	(9) 28.3 [0.89] 27.1 29.8
U-M										(7) 27.7 [1.25] 25.2 28.6	(58) 28.2 [1.70] 24.6 32.3	(14) 28.6 [1.90] 25.8 31.1
U-U							(2) 29.0 28.2 29.8					

Bobolink

Dolichonyx oryzivorus

n = 1

(1) HY-U, Sept., 34.3.

Eastern Meadowlark

Sturnella magna

n = 7

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(1) 86.1	(1) 78.5						
AHY-U				(4) 101.7 83.6 119.5	(1) 118.2							

Red-winged Blackbird					<i>Agelaius phoeniceus</i>					n = 625		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F										(18) 44.2 [2.89] 39.0 48.1	(28) 45.4 [3.69] 37.5 53.0	(1) 47.3
HY-M										(6) 66.8 [9.06] 55.5 80.3	(21) 69.5 [4.19] 63.1 77.7	(6) 63.1 [6.01] 53.6 68.8
HY-U							(1) 33.0				(3) 44.5 41.1 47.5	(1) 47.3
AHY-F			(6) 44.2 [2.27] 41.4 46.4	(62) 41.4 [3.32] 29.0 55.0	(130) 40.7 [2.49] 36.2 48.3	(9) 40.8 [2.44] 37.6 44.2	(4) 37.2 35.6 40.4			(3) 42.0 40.1 45.6	(11) 45.4 [3.30] 40.0 50.5	
AHY-M			(2) 65.0 64.2 65.8	(8) 63.6 [6.43] 52.9 71.8	(6) 61.8 [2.93] 57.7 66.5					(1) 64.1	(15) 71.6 [4.03] 62.7 78.2	
SY-M	(1) 67.2		(13) 64.2 [4.73] 57.6 72.8	(103) 61.9 [3.11] 54.1 69.4	(69) 63.1 [3.38] 57.0 74.9	(7) 59.0 [3.01] 54.0 62.7	(7) 60.9 [2.53] 57.1 64.7					
ASY-F				(3) 41.1 40.2 42.6	(3) 41.5 39.8 42.4							
ASY-M			(11) 64.2 [3.28] 59.6 72.1	(32) 66.7 [3.50] 58.2 72.1	(12) 63.6 [2.66] 61.1 70.6						(3) 76.9 71.5 81.1	
U-F										(8) 45.9 [4.08] 37.1 48.4	(9) 43.8 [3.86] 41.0 52.4	(1) 51.0
U-U										(1) 44.6		

Orchard Oriole

Icterus spurius

n = 15

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 20.0				
HY-U							(3) 22.6 22.0 23.1	(1) 25.6				

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F					(4) 20.2 18.8 21.9		(1) 19.5					
SY-M					(4) 22.4 20.6 24.1			(1) 23.5				
Northern Oriole (Baltimore Oriole)					<i>Icterus galbula</i>					n = 131		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 34.3				
HY-M									(2) 35.8 34.9 36.7			
HY-U						(1) 32.0	(2) 29.0 28.4 29.6	(9) 33.0 [3.00] 30.0 38.9				
AHY-F					(49) 33.2 [2.87] 28.1 41.3	(1) 32.4	(1) 30.8	(1) 38.4	(1) 33.2			
AHY-M				(1) 35.0	(24) 33.4 [3.60] 22.3 41.5	(2) 37.0 35.1 38.8		(1) 40.0	(3) 37.3 36.6 38.3			
SY-M					(9) 33.8 [2.53] 31.3 36.2	(2) 34.0 32.4 35.7		(1) 29.2				
ASY-F					(5) 32.6 [4.70] 28.1 38.7							
ASY-M					(14) 35.2 [2.51] 31.1 40.0							
U-F								(1) 34.9				
Rusty Blackbird					<i>Euphagus carolinus</i>					n = 245		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F										(11) 56.6 [4.61] 47.3 64.0	(9) 54.8 [4.66] 47.1 61.3	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M										(6) 63.8 [4.11] 58.5 70.3	(13) 65.1 [3.06] 59.3 69.3	
HY-U										(1) 52.9		
AHY-F			(17) 54.0 [3.31] 49.1 59.7	(53) 54.6 [5.20] 47.0 76.5	(4) 56.0 54.7 58.0					(11) 55.7 [6.42] 47.7 70.4	(7) 58.1 [2.59] 54.1 61.0	
AHY-M	(1) 64.8		(33) 63.1 [4.16] 45.9 69.3	(35) 63.6 [4.51] 52.4 76.8						(5) 70.6 [3.59] 64.9 74.5	(7) 69.8 [6.76] 60.6 80.4	
AHY-U			(3) 54.5 53.1 57.1	(1) 61.1						(2) 61.8 58.5 65.2		
U-F										(5) 57.6 [4.69] 51.3 64.1	(8) 57.1 [4.24] 53.5 66.3	
U-M										(7) 61.0 [5.08] 55.1 69.1	(3) 68.7 66.5 71.2	
U-U										(3) 57.5 54.3 63.7		
Common Grackle										<i>Quiscalus quiscula</i>		
										n = 215		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F										(14) 93.4 [5.06] 83.2 101.0	(1) 86.1	
HY-M										(13) 117.3 [10.37] 90.4 136.4		
HY-U						(9) 89.0 [8.39] 75.4 102.0	(6) 94.1 [12.64] 78.2 112.4	(3) 104.2 84.5 132.1		(1) 120.4		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F			(1) 87.8	(8) 101.7 [5.83] 95.4 113.9	(18) 98.1 [11.53] 82.1 124.7	(11) 91.9 [4.28] 85.6 99.1	(2) 97.7 95.5 99.9			(2) 96.2 94.9 97.6		
AHY-M				(11) 122.4 [12.88] 96.7 135.4	(76) 118.9 [6.92] 90.9 136.9	(13) 120.9 [9.86] 90.4 131.4	(3) 130.6 116.2 144.8			(3) 118.2 107.5 126.0		
SY-M				(1) 118.1								
ASY-M				(4) 121.0 96.5 138.5								
U-F										(11) 95.4 [5.06] 89.1 103.5		
U-M										(3) 118.6 117.1 119.5		
U-U										(1) 94.5		

(Note: the extreme variation in weights and the large standard deviations in the grackle sample may be the result of incorrectly aged or sexed birds.)

Brown-headed Cowbird			<i>Molothrus ater</i>								n = 1476	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(1) 32.6	(1) 35.5	(1) 37.5	(3) 40.5 38.1 44.4	
HY-U							(8) 35.2 [4.30] 31.2 42.2	(8) 35.1 [5.45] 30.4 45.4				
AHY-F			(7) 40.4 [2.18] 37.9 43.9	(299) 37.8 [2.39] 32.4 49.2	(275) 39.7 [3.09] 30.5 51.2	(5) 39.0 [2.13] 37.0 41.8	(3) 38.6 35.5 40.6				(1) 34.5	
AHY-M			(2) 53.0 52.1 53.8	(38) 48.4 [2.21] 32.4 49.2	(51) 48.8 [4.37] 36.0 57.4				(1) 44.5	(1) 47.6		
AHY-U				(1) 37.6	(1) 31.8							

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
SY-M			(9) 49.3 [2.20] 45.5 52.7	(198) 49.2 [3.41] 34.4 57.5	(144) 48.6 [2.78] 39.8 57.4	(1) 49.4						
ASY-F				(39) 38.0 [2.78] 32.9 47.2	(58) 40.5 [2.79] 33.2 45.5	(3) 41.3 40.2 42.2						
ASY-M			(4) 51.2 45.8 54.3	(169) 48.8 [3.08] 39.7 58.0	(133) 49.3 [3.05] 43.3 56.6	(6) 49.2 [2.73] 46.2 52.7						
U-F									(1) 33.1		(1) 30.5	
U-U								(1) 31.9	(2) 37.6 36.8 38.4			
Scarlet Tanager <i>Piranga olivacea</i> n = 544												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(3) 24.5 23.5 25.1	(32) 28.3 [1.57] 23.4 30.8	(100) 28.5 [1.78] 24.5 33.5	(2) 30.7 27.8 33.5		
HY-M							(9) 28.3 [1.53] 26.2 31.3	(33) 28.3 [1.57] 24.3 31.4	(133) 29.5 [1.75] 26.4 36.0	(7) 29.2 [3.54] 24.2 34.5		
HY-U								(1) 26.9	(5) 28.5 [2.18] 26.1 31.6	(1) 29.0		
AHY-F					(39) 27.9 [2.57] 21.8 35.1	(8) 30.3 [2.83] 25.8 29.8 35.2	(4) 28.4 25.8 29.8	(6) 28.8 [1.09] 27.2 30.0	(9) 27.2 [2.74] 21.5 30.5	(1) 31.1		
AHY-M					(10) 28.5 [1.24] 26.6 30.6			(2) 27.1 26.3 27.9	(15) 30.3 [2.32] 27.6 33.5			
AHY-U								(1) 25.8				
SY-F					(2) 27.0 26.3 27.7							

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
SY-M					(23) 28.2 [1.56] 26.2 31.9	(3) 28.3 28.0 28.6	(1) 28.7	(2) 29.1 27.2 30.9				
ASY-M					(18) 28.3 [2.41] 24.4 34.3	(2) 27.3 27.0 27.5	(1) 28.7	(3) 31.6 29.7 34.6				
TY-M							(1) 29.3					
ATY-M					(2) 29.5 27.6 31.4							
U-F								(9) 28.1 [1.18] 26.4 30.4	(27) 28.9 [1.78] 25.0 33.6			
U-M								(4) 28.0 27.1 28.8	(24) 29.3 [3.26] 17.5 33.1			
U-U									(1) 30.3			
Summer Tanager					<i>Piranga rubra</i>					n = 4		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
SY-M				(1) 25.5	(3) 29.2 27.2 31.2							
Cardinal					<i>Cardinalis cardinalis</i>					n = 1471		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(8) 38.4 [3.22] 34.7 42.5	(39) 39.1 [2.89] 31.7 43.9	(55) 40.5 [2.34] 34.4 44.0	(59) 40.5 [2.48] 30.7 46.2	(38) 40.6 [2.20] 35.4 45.0	(3) 49.7 43.3 58.2
HY-M							(6) 42.4 [3.25] 38.6 47.7	(17) 41.5 [2.84] 35.9 46.1	(35) 42.1 [3.04] 34.9 51.8	(48) 42.4 [3.24] 32.1 48.7	(29) 43.8 [2.80] 38.8 48.4	(4) 46.0 44.8 47.1
HY-U							(2) 37.5 35.4 39.5	(6) 42.7 [3.47] 38.3 48.5	(12) 42.2 [2.86] 35.6 46.2	(2) 42.0 42.4		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F	(29) 49.3 [4.68] 40.1 64.9	(21) 47.8 [3.88] 39.3 54.3	(112) 44.6 [3.62] 36.9 52.7	(63) 41.1 [2.61] 35.4 47.6	(18) 41.4 [2.28] 37.0 45.8		(5) 43.1 [1.58] 42.0 45.7	(3) 41.4 39.1 44.0	(4) 38.5 36.6 39.9	(13) 42.2 [1.88] 38.6 45.3	(12) 42.3 [2.44] 38.7 47.0	(10) 49.9 [4.91] 43.6 60.5
AHY-M	(27) 51.6 [4.11] 45.0 63.2	(15) 48.3 [4.25] 43.0 57.2	(100) 46.3 [3.48] 38.3 57.5	(51) 43.2 [3.29] 34.0 51.0	(24) 41.6 [2.72] 34.4 46.2		(2) 43.6 42.3 44.9	(1) 37.7 42.2 48.8	(4) 44.2 [2.49] 40.3 48.1	(17) 43.4 [3.48] 39.1 50.2	(13) 45.1 [4.34] 42.6 57.5	(21) 51.2 [4.34] 42.6 57.5
SY-F	(22) 46.1 [3.93] 40.3 57.3	(5) 44.4 [0.94] 43.5 45.7	(43) 43.7 [3.34] 36.0 52.1	(18) 41.3 [4.35] 36.0 47.2	(9) 40.5 [3.48] 36.3 46.0		(1) 39.5		(2) 41.2 36.0 46.4	(1) 39.9	(2) 42.2 41.3 43.1	
SY-M	(29) 47.5 [4.19] 41.4 56.3	(11) 46.2 [3.34] 40.8 50.6	(61) 46.2 [3.75] 37.7 53.3	(23) 41.9 [2.52] 37.0 47.2	(8) 40.4 [1.73] 38.5 43.0		(1) 41.6	(1) 40.9	(2) 43.1 40.7 45.5	(1) 47.6	(5) 45.2 [1.17] 43.6 46.1	(1) 41.0
ASY-F	(4) 44.6 41.4 47.8	(5) 47.4 [3.19] 42.9 50.3	(13) 44.4 [2.46] 40.9 48.1	(4) 43.5 41.4 49.4	(1) 42.2			(1) 44.2			(1) 44.8	(1) 43.5
ASY-M	(9) 49.0 [2.91] 42.9 52.5	(7) 49.5 [3.32] 45.2 53.6	(14) 46.2 [2.10] 43.1 49.4	(12) 40.6 [1.55] 37.8 43.1	(3) 42.0 40.1 44.3		(1) 40.8		(1) 38.8	(2) 47.1 46.2 48.0		
TY-F	(2) 46.6 45.9 47.2	(2) 49.9 48.5 51.2	(2) 44.1 43.7 44.5	(2) 42.8 42.2 43.3	(1) 50.1			(1) 45.0	(1) 42.6			
TY-M	(1) 52.8		(5) 44.7 [1.35] 43.0 46.4	(3) 42.8 42.3 43.2	(4) 44.9 42.4 50.2						(3) 47.8 42.9 50.4	
ATY-F	(7) 46.0 [2.86] 42.4 50.1	(4) 44.9 42.1 47.8	(19) 44.0 [2.63] 41.0 50.9	(7) 41.9 [4.86] 33.6 49.2	(2) 43.0 42.7 43.3		(1) 42.2		(4) 42.5 40.3 43.6		(4) 41.7 41.0 43.2	(3) 46.3 45.3 47.0
ATY-M	(5) 46.9 [1.16] 45.5 48.2	(9) 48.7 [5.01] 42.0 55.0	(33) 45.6 [2.73] 40.8 51.4	(17) 43.0 [2.97] 38.0 50.7	(9) 43.3 [2.34] 39.5 47.9	(3) 43.7 43.3 44.1		(1) 38.9	(4) 41.8 38.8 44.5	(1) 41.8	(4) 45.1 42.1 47.1	(1) 46.3
U-F									(1) 45.2	(17) 40.8 [3.69] 34.6 45.3	(5) 42.2 [3.05] 39.5 47.3	(9) 45.5 [3.63] 41.3 51.2

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-M									(1) 42.6	(10) 41.6 [3.16] 33.7 45.2	(9) 43.4 [3.46] 36.6 48.1	(1) 53.7
Rose-breasted Grosbeak <i>Phoeucticus ludovicianus</i> n = 494												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(4) 41.4 37.7 45.0	(14) 41.7 [1.77] 39.0 45.3	(70) 45.4 [3.68] 33.8 56.0	(7) 47.9 [3.14] 43.3 52.2		
HY-M							(4) 39.0 36.7 41.3	(21) 40.8 [3.30] 32.8 48.6	(88) 45.0 [3.63] 37.5 53.4	(7) 54.5 [6.76] 46.3 63.0		
HY-U							(1) 40.6					
AHY-F					(67) 46.2 [4.13] 38.3 56.1		(4) 41.8 40.7 43.3	(7) 41.6 [3.51] 35.4 46.8	(21) 45.4 [4.37] 38.7 52.6	(1) 62.4		
AHY-M					(2) 41.0 39.9 42.1			(6) 41.1 [4.44] 36.9 49.2	(20) 48.3 [3.15] 43.3 55.4	(2) 49.0 47.6 50.5		
SY-M				(2) 43.7 42.2 45.3	(28) 44.4 [4.24] 37.3 52.5		(1) 40.5	(8) 43.7 [1.83] 39.7 45.7	(2) 46.7 46.6 46.8			
ASY-M				(2) 44.9 44.1 45.7	(59) 46.3 [4.80] 38.6 57.5		(5) 40.3 [2.40] 36.3 42.5					
TY-M					(1) 41.9	(1) 43.0						
ATY-M					(2) 42.7 42.3 43.1				(1) 40.5			
U-F								(1) 40.2	(29) 45.9 [4.00] 38.5 56.3	(2) 58.5 52.1 65.0		
U-M									(3) 46.6 42.2 49.5			
U-U								(1) 43.2				

Indigo Bunting											
<i>Passerina cyanea</i>											
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	n = 1288
HY-F							(2)	(32)	(101)	(16)	
							13.7	13.8	14.2	15.9	
							13.1	[0.98]	[1.26]	[2.30]	
							14.2	12.2	11.7	12.9	
HY-M								16.7	20.0	19.9	
							(10)	(22)	(65)	(8)	
							14.2	14.5	14.6	15.2	
							[0.87]	[1.14]	[1.05]	[1.48]	
HY-U							13.0	12.0	12.5	13.2	
							16.1	16.5	19.0	17.8	
							(29)	(71)	(76)	(16)	
							14.1	14.7	14.4	14.6	
AHY-F							[0.96]	[1.26]	[1.00]	[0.88]	
							12.5	12.2	11.6	13.5	
							16.2	17.7	16.9	17.1	
					(137)	(29)	(35)	(25)	(33)	(12)	
AHY-M					13.7	14.2	14.1	13.8	14.8	15.9	
					[0.97]	[1.16]	[1.24]	[1.38]	[1.20]	[1.64]	
					11.4	12.1	12.4	11.5	12.7	13.8	
					18.0	17.2	17.5	18.0	18.3	18.5	
SY-F				(1)	(50)	(6)	(9)	(10)	(52)	(14)	
				16.7	14.7	14.1	14.4	15.0	16.1	16.5	
					[0.88]	[0.80]	[0.92]	[0.73]	[1.77]	[1.38]	
					13.0	13.2	13.1	14.1	13.4	14.4	
SY-M					16.7	15.3	15.9	16.4	21.4	18.5	
					(2)	(2)	(2)	(3)			
					15.2	14.4	12.8	12.2			
					13.6	13.7	12.3	11.4			
ASY-F					16.7	15.1	13.2	13.6			
					(101)	(23)	(19)	(4)	(7)		
					14.5	14.5	14.5	14.5	15.3		
					[0.92]	[0.96]	[0.70]	13.0	[1.81]		
ASY-M					12.7	12.8	12.8	15.4	13.3		
					16.7	17.3	15.6		18.8		
					(6)	(2)	(5)	(5)	(1)		
					13.7	14.4	13.0	13.8	16.6		
TY-F					[0.74]	14.4	[1.83]	[0.83]			
					12.5	14.4	11.2	12.7			
					14.5		15.8	14.7			
					(2)	(5)	(1)	(10)	(3)		
TY-M					15.0	14.7	14.8	15.6	15.4	16.1	
					14.2	[0.94]	[0.64]		[0.98]	15.2	
					15.8	13.1	14.2		14.0	16.7	
					17.2	15.9		16.8			
TY-F					(3)	(2)	(1)	(3)			
					13.7	14.1	13.6	13.2			
					12.7	13.9		12.7			
					15.4	14.2		13.8			
TY-M					(13)	(5)	(4)	(5)	(3)		
					14.7	14.5	14.8	14.4	14.8		
					[0.55]	[0.70]	14.4	[0.59]	12.6		
					14.0	13.7	15.2	13.4	16.2		
					15.6	15.2		14.9			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ATY-F					(14) 14.4 [1.69] 12.6 18.5	(1) 18.6	(4) 14.0 13.4 14.6	(6) 15.0 [0.93] 13.6 16.3	(5) 14.5 [1.02] 13.5 16.1	(1) 13.7		
ATY-M					(45) 14.5 [1.30] 12.3 20.7	(3) 13.9 13.8 14.1 15.9	(7) 14.7 [0.72] 13.7 15.9	(7) 15.4 [0.76] 13.8 16.0	(12) 16.2 [1.87] 14.3 20.1			
U-M					(2) 16.4 15.0 17.7			(1) 14.5				
U-U								(8) 14.2 [0.90] 13.1 15.9	(27) 14.9 [0.96] 13.2 16.8	(2) 16.0 14.5 17.4		
Evening Grosbeak	<i>Hesperiphona vespertina</i>										n = 2047	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F											(3) 56.4 54.7 57.3	(22) 61.2 [4.21] 55.8 70.6
HY-M											(2) 61.3 57.0 65.6	(11) 59.1 [4.23] 51.6 64.3
AHY-F	(77) 60.5 [3.77] 51.8 72.5	(111) 60.7 [4.17] 52.6 70.1	(227) 59.5 [4.00] 47.0 69.8	(138) 58.2 [4.61] 43.2 73.0	(21) 63.3 [5.01] 57.3 73.2						(1) 56.3	(33) 59.3 [3.33] 51.5 65.6
AHY-M	(59) 61.5 [3.51] 53.7 70.3	(100) 62.0 [4.16] 51.2 72.1	(151) 60.1 [3.88] 49.7 70.2	(87) 59.3 [5.61] 45.4 86.1	(20) 66.8 [5.96] 54.9 77.7						(3) 60.9 55.3 65.2	(75) 62.0 [3.93] 54.8 73.4
SY-F	(8) 58.9 [1.82] 56.0 62.0	(4) 64.1 58.7 68.8	(92) 56.5 [7.25] 46.5 68.6	(124) 56.3 [4.08] 45.5 68.3	(4) 62.4 53.2 70.3							
SY-M	(1) 60.3		(37) 56.9 [2.90] 51.4 65.0	(97) 57.9 [3.26] 51.0 69.3	(5) 59.7 [4.01] 55.1 63.3							
ASY-F	(5) 58.3 [1.52] 55.8 59.7	(8) 61.1 [3.47] 57.5 68.6	(110) 57.9 [3.83] 51.1 70.8	(118) 57.6 [4.35] 49.0 73.5	(7) 62.2 [7.11] 52.1 69.6							

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U			(2) 11.7 11.5 11.9	(3) 15.0 13.1 16.6								
ASY-M			(1) 14.6	(6) 15.0 [1.03] 13.6 16.5								
<i>Carduelis pinus</i>												
Pine Siskin											n = 356	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U										(25) 13.5 [1.24] 11.7 16.8	(3) 12.3 12.2 12.6	
AHY-U	(7) 16.2 [1.17] 15.0 18.6	(11) 17.6 [1.20] 16.0 20.1	(132) 15.1 [1.31] 12.1 19.0	(111) 14.1 [1.18] 11.8 19.0	(21) 14.5 [1.75] 12.1 18.7				(1) 12.3	(13) 13.4 [1.38] 10.8 15.6	(4) 13.6 11.6 15.3	
U-U										(16) 12.9 [0.79] 11.3 14.1	(12) 13.5 [0.60] 12.5 14.7	
<i>Carduelis tristis</i>												
American Goldfinch											n = 5180	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F								(2) 11.7 11.2 12.2	(110) 11.4 [0.92] 8.6 13.7	(269) 12.1 [0.81] 9.7 14.5	(79) 12.7 [0.87] 10.9 14.9	(2) 15.0 14.1 15.8
HY-M								(6) 12.1 [0.86] 11.0 13.4	(116) 12.0 [1.08] 9.4 15.3	(226) 12.4 [0.80] 9.6 14.8	(68) 13.1 [1.03] 10.5 16.3	(1) 13.8
HY-U								(13) 11.7 [1.12] 9.8 13.7	(223) 11.8 [0.97] 8.4 14.8	(101) 12.2 [0.80] 10.1 13.9	(135) 12.8 [0.88] 10.5 15.1	
AHY-F	(7) 14.2 [1.20] 13.4 16.8	(6) 14.1 [1.12] 12.7 15.6	(74) 13.6 [1.00] 11.8 17.1	(158) 13.2 [0.81] 10.5 15.7	(520) 12.4 [0.90] 10.3 16.5	(24) 12.1 [0.72] 10.6 13.5	(15) 12.5 [0.60] 11.6 13.4	(122) 12.5 [0.90] 10.7 15.3	(281) 12.4 [0.85] 10.0 15.2	(152) 12.5 [0.76] 10.4 15.0	(133) 12.9 [0.97] 10.4 16.1	
AHY-M	(9) 14.5 [0.80] 13.0 15.8	(14) 15.4 [1.35] 13.6 18.8	(142) 14.2 [1.05] 11.5 17.1	(257) 13.9 [0.83] 11.6 16.6	(327) 12.6 [1.03] 10.6 17.1	(17) 11.9 [0.63] 10.5 13.0	(11) 11.9 [0.47] 11.1 13.0	(129) 12.5 [0.83] 10.5 14.6	(264) 13.0 [0.86] 10.0 15.4	(158) 13.3 [1.00] 10.5 19.4	(189) 13.4 [0.88] 11.5 19.4	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U			(7) 14.2 [1.02] 12.9 15.5	(3) 13.6 13.1 14.5	(4) 12.3 11.6 13.3				(3) 10.9 9.0 12.0	(4) 12.6 12.2 13.2	(6) 12.9 [0.46] 12.4 13.7	
SY-F					(1) 11.2			(1) 11.2				
SY-M	(1) 14.0		(46) 14.3 [0.93] 12.6 17.1	(83) 13.6 [0.90] 12.1 16.3	(159) 12.7 [1.00] 8.6 16.2	(5) 11.6 [0.63] 10.8 12.4	(2) 11.3 10.9 11.6	(10) 12.7 [0.78] 11.2 13.9	(22) 12.7 [0.85] 11.1 14.2	(3) 13.4 13.0 14.0		
ASY-F					(11) 11.9 [0.74] 10.6 13.1			(10) 12.2 [0.48] 11.4 12.9	(8) 12.2 [0.67] 11.0 13.0	(1) 10.7	(2) 13.1 12.6 13.5	
ASY-M	(1) 13.4	(1) 20.7	(30) 14.3 [1.02] 12.6 16.4	(92) 13.9 [0.91] 11.6 17.6	(107) 12.8 [1.13] 9.2 15.6	(2) 12.6 11.9 13.3	(3) 12.3 12.0 12.5	(10) 12.6 [0.48] 11.7 13.3	(19) 12.8 [0.83] 11.5 14.3	(1) 13.0	(1) 9.9	
TY-F					(1) 13.3					(1) 13.3		
ATY-F			(2) 12.8 12.6 12.9	(1) 12.8	(4) 12.1 11.2 12.7	(2) 12.1 11.7 12.4	(1) 12.8	(3) 12.2 11.5 13.4		(4) 11.9 11.4 12.3		
ATY-M		(1) 15.2	(3) 13.3 12.5 13.9	(5) 14.3 [1.30] 12.4 15.4	(17) 11.9 [0.67] 11.0 13.3	(3) 12.3 11.7 12.7	(1) 12.7	(10) 12.7 [0.73] 11.7 14.2	(8) 12.7 [0.45] 11.8 13.4	(4) 12.8 11.9 13.9	(3) 13.5 11.8 14.7	
U-F									(1) 11.6		(1) 11.5	
U-M									(1) 11.6	(6) 13.0 [0.92] 12.2 14.1		(1) 13.7
U-U								(1) 11.7	(8) 12.0 [0.91] 10.5 13.2	(48) 12.4 [1.14] 10.2 15.5	(20) 12.9 [0.68] 10.9 13.8	

Rufous-sided Towhee

Pipilo erythrophthalmus

n = 711

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(5) 36.3 [2.08] 33.9 39.1	(16) 36.8 [1.82] 34.5 41.2	(42) 39.7 [2.10] 35.7 44.5	(98) 39.1 [2.64] 30.8 47.6	(4) 39.7 37.2 43.1	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-M					(1) 40.4	(1) 41.3	(8) 38.5 [2.66] 35.5 42.3	(36) 39.0 [2.12] 34.8 44.5	(62) 42.7 [3.45] 29.3 51.5	(102) 42.8 [2.59] 35.7 49.0	(3) 48.4 42.5 51.5	
AHY-F				(21) 38.0 [2.98] 33.7 46.8	(31) 38.6 [4.16] 32.1 52.3	(2) 40.7 40.0 41.4	(2) 36.5 34.3 38.7	(6) 39.5 [1.86] 37.9 43.1	(14) 39.6 [2.26] 36.2 43.6	(37) 39.9 [2.88] 33.9 44.7		
AHY-M			(6) 42.9 [2.31] 39.4 45.8	(15) 40.7 [1.95] 38.4 45.6	(15) 40.2 [2.37] 36.1 46.5	(1) 40.4	(3) 45.5 43.4 47.4	(3) 41.3 39.6 42.2	(8) 42.8 [2.31] 39.2 45.9	(33) 43.0 [2.99] 37.8 50.0		
SY-M			(4) 42.8 42.3 43.5 44.5	(35) 40.9 [2.26] 36.9 44.5	(21) 40.6 [3.26] 32.1 45.2	(3) 41.3 40.4 42.3	(3) 42.2 38.8 44.7	(2) 41.4 39.7 43.4	(2) 44.7 44.7 44.7	(2) 42.0 41.4 42.6		
ASY-F					(2) 36.2 34.0 38.4			(1) 40.5	(1) 42.7			
ASY-M			(2) 40.8 37.8 43.8	(19) 41.8 [2.03] 37.9 45.0	(10) 41.4 [1.63] 39.0 43.9	(1) 42.5		(1) 40.4	(1) 41.3			
TY-M				(3) 40.3 38.6 43.6	(3) 43.1 42.2 43.9					(1) 43.2		
ATY-F				(4) 39.5 33.6 43.1	(2) 40.2 39.5 40.9							
ATY-M			(1) 48.2	(1) 39.5	(2) 40.6 39.5 41.7					(2) 47.8 47.1 48.5		
U-F									(1) 45.4	(3) 39.5 37.4 40.9		(1) 50.4
U-M										(2) 45.1 44.1 46.1		

Savannah Sparrow

Passerculus sandwichensis

n = 60

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(1) 15.6	(5) 18.1 [0.42] 17.4 18.5	(5) 19.3 [2.09] 16.9 22.3		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U			(19) 18.3 [1.27] 15.4 20.3	(10) 18.6 [1.85] 16.1 23.0	(2) 17.3 16.2 18.4				(1) 16.8	(1) 17.2		
U-U								(4) 16.0 14.9 17.4	(11) 16.7 [1.93] 12.4 20.5	(1) 21.9		

Grasshopper Sparrow

Ammodramus savannarum

n = 21

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(4) 16.6 15.4 17.8	(2) 16.1 15.7 16.5	(2) 19.0 17.0 21.0		
AHY-M					(1) 16.6							
AHY-U					(6) 16.1 [0.90] 15.1 17.3							
U-U									(4) 16.3 15.3 17.4	(2) 17.2 16.7 17.6		

Henslow's Sparrow

Ammodramus henslowii

n = 4

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(2) 13.8 11.7 15.9		(1) 12.3		
U-U										(1) 12.2		

Vesper Sparrow

Pooecetes gramineus

n = 21

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(1) 26.3	(2) 22.6 22.0 23.1	(1) 21.5		
AHY-F					(1) 22.2							
AHY-M					(2) 25.0 24.7 25.2							
AHY-U			(2) 25.8 25.4 26.2	(5) 23.6 [1.36] 22.0 25.4	(3) 24.5 21.8 26.2					(1) 24.3		

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-U									(3) 25.4 24.6 26.1			.
Dark-eyed Junco (Slate-colored Junco)					<i>Junco hyemalis</i>					n = 7715		
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F										(111) 17.9 [1.08] 15.0 21.3	(136) 18.0 [1.30] 15.5 22.1	(7) 19.9 [1.39] 17.9 21.9
HY-M										(67) 19.5 [1.10] 17.2 23.4	(132) 20.0 [1.48] 15.6 23.6	(2) 23.3 21.9 24.6
HY-U									(5) 18.0 [0.90] 16.9 19.4	(268) 18.6 [1.31] 15.6 22.8	(269) 19.5 [1.39] 16.3 25.8	(14) 21.1 [1.33] 18.2 23.2
AHY-F	(24) 21.2 [1.64] 18.2 24.9	(6) 20.5 [0.79] 19.4 21.5	(213) 19.1 [1.41] 14.3 23.4	(776) 18.7 [1.51] 14.6 23.6	(4) 20.1 18.1 22.2				(1) 17.4 [1.22] 14.4 21.2	(169) 18.2 [1.13] 16.1 21.3	(94) 18.9 [1.13] 16.1 21.3	(4) 21.0 18.5 25.1
AHY-M	(28) 22.7 [1.52] 20.0 25.6	(13) 22.0 [1.26] 19.9 24.0	(1016) 20.6 [1.53] 16.4 25.4	(982) 20.4 [1.61] 16.3 26.7					(1) 18.6 [1.21] 14.3 23.1	(418) 19.5 [1.42] 15.5 25.1	(285) 20.2 [1.20] 20.5 24.2	(13) 22.2 [1.20] 20.5 24.2
AHY-U	(23) 22.3 [1.15] 20.4 26.0	(11) 22.1 [2.30] 18.1 26.2	(790) 20.0 [1.54] 13.5 25.3	(951) 19.5 [1.53] 14.2 25.1	(6) 19.7 [1.15] 17.9 21.0				(3) 19.4 18.8 20.2 22.6	(313) 18.6 [1.29] 13.6 22.6	(171) 19.7 [1.18] 17.0 23.1	(4) 21.4 19.6 23.4
SY-F	(1) 23.0		(2) 19.4 18.6 20.1	(1) 17.7								
SY-M				(1) 22.6							(1) 20.1	
SY-U	(3) 22.2 21.8 22.5		(6) 19.4 [1.28] 17.0 20.3	(3) 20.8 19.6 21.5								
ASY-F			(6) 19.3 [0.28] 19.0 19.7	(3) 21.0 20.3 21.6								
ASY-M	(1) 23.4		(16) 20.7 [1.32] 18.7 23.0	(9) 20.7 [1.54] 17.4 22.6						(3) 18.8 17.4 19.9	(5) 19.8 [1.24] 20.7	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-U	(3) 20.9 20.2 21.5		(5) 19.6 [0.98] 18.0 20.6	(6) 19.4 [1.50] 17.7 21.3								(1) 19.1
ATY-M	(4) 20.8 19.3 22.0			(5) 22.0 [0.67] 21.5 23.1						(1) 18.7	(1) 18.7	
ATY-U	(1) 22.2		(7) 21.0 [0.61] 20.2 22.0									
U-F											(9) 19.6 [1.27] 18.5 22.3	(3) 21.5 20.7 22.1
U-M											(13) 20.4 [1.47] 18.1 23.3	(3) 21.2 20.1 22.9
U-U										(138) 18.5 [1.47] 12.9 22.7	(115) 19.2 [1.29] 13.9 22.0	(9) 20.6 [1.90] 18.0 23.0
Dark-eyed Junco hybrids (Slate-colored × Oregon)												
<i>Junco h. hyemalis</i> × <i>J. h. montanus</i>												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F											(1) 18.0	
HY-U											(2) 17.5 17.2 17.8	
AHY-F			(1) 18.7	(1) 20.1								
AHY-U			(5) 19.7 [0.56] 19.1 20.6	(34) 18.8 [1.41] 16.4 21.7								
Dark-eyed Junco (Oregon Junco)												
<i>Junco hyemalis montanus</i>												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-F			(1) 22.5									
AHY-M	(1) 21.1											
AHY-U										(1) 16.5		

Tree Sparrow

Spizella arborea

n = 1585

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U										(2) 15.8 15.3 16.2	(78) 16.9 [1.16] 13.8 19.7	
AHY-U	(169) 18.9 [1.56] 15.7 25.6	(105) 19.4 [1.33] 16.5 22.5	(590) 18.5 [1.51] 14.2 23.7	(153) 18.4 [1.73] 14.0 25.7	(2) 19.7 18.1 21.3					(4) 17.2 15.3 19.1	(160) 17.3 [1.25] 14.5 20.5	(11) 17.8 [1.64] 15.4 21.2
SY-U	(3) 18.6 17.3 20.0	(4) 19.0 17.7 21.7	(6) 18.8 [1.29] 20.4	(5) 17.9 [1.05] 16.8 19.5								
ASY-U	(6) 18.5 [0.87] 17.0 19.5	(8) 18.8 [1.14] 17.6 20.2	(37) 18.7 [1.28] 16.1 21.2	(12) 18.5 [2.01] 15.2 22.2							(7) 17.6 [0.99] 16.0 18.9	(1) 16.9
TY-U	(2) 18.9 18.6 19.1		(4) 18.7 17.6 21.1									
ATY-U	(5) 19.2 [0.90] 18.2 20.6	(6) 19.8 [0.70] 18.5 20.4	(40) 18.6 [1.45] 15.1 21.3	(9) 19.2 [2.23] 16.5 22.6							(5) 17.9 [1.31] 16.0 19.5	
U-U										(1) 16.4	(98) 17.8 [1.49] 14.0 22.7	(52) 18.9 [1.75] 15.6 23.9

Chipping Sparrow

Spizella passerina

n = 1143

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U						(5) 12.3 [0.17] 12.2 12.6	(2) 12.4 11.7 13.0 13.7	(9) 11.5 [1.12] 10.1 13.7	(75) 12.1 [0.84] 10.1 14.7	(115) 12.4 [0.92] 10.5 15.4	(3) 13.2 12.5 13.8	
AHY-F				(2) 13.6 13.5 13.7	(14) 12.4 [1.17] 10.6 14.6	(6) 11.8 [1.29] 10.5 14.0	(1) 12.7 11.4	(1)				
AHY-M				(15) 12.3 [0.57] 11.5 13.4	(53) 11.9 [0.81] 9.9 13.9	(5) 12.5 [0.57] 11.5 12.9			(2) 12.2 11.1 13.2			

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U			(2) 13.8 13.3 14.2	(361) 12.3 [1.07] 10.1 18.8	(316) 11.7 [0.87] 9.8 15.1	(1) 12.5	(1) 12.9	(1) 11.9	(17) 12.2 [0.66] 11.4 14.0	(46) 12.7 [0.83] 11.1 14.3	(2) 12.3 12.0 12.6	
SY-U				(6) 12.2 [0.42] 11.9 12.9	(4) 12.4 11.9 12.8							
ASY-F				(1) 11.7	(1) 13.7	(1) 12.7						
ASY-M				(8) 12.4 [0.68] 11.7 13.6	(13) 12.4 [0.62] 11.1 13.1	(1) 12.5						
ASY-U				(28) 12.5 [0.67] 11.2 14.3	(15) 12.5 [0.67] 11.5 13.9				(1) 11.9	(4) 12.8 11.7 14.5		
U-U										(3) 12.4 11.7 12.8	(1) 12.6	(1) 12.4
Field Sparrow	<i>Spizella pusilla</i>										n = 4778	
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(1) 10.2	(1) 12.8		(2) 12.5 12.4 12.6		
HY-M							(1) 12.8	(2) 11.7 11.5 11.8	(1) 12.3	(3) 12.1 11.2 13.5	(4) 12.4 11.3 13.3	
HY-U						(3) 11.6 9.2 12.8	(128) 12.0 [0.72] 10.2 14.3	(222) 12.0 [0.94] 10.0 15.7	(189) 12.6 [0.95] 10.3 15.7	(1057) 12.9 [0.92] 9.0 17.2	(103) 13.2 [1.14] 10.9 16.5	
AHY-F			(1) 13.4	(4) 12.1 11.4 12.9	(44) 12.6 [1.15] 11.0 15.9	(17) 12.9 [1.19] 10.3 14.7	(22) 12.1 [1.34] 10.4 16.5	(32) 12.1 [0.76] 11.2 14.0	(12) 12.6 [0.93] 11.1 14.4	(8) 11.9 [0.94] 10.4 13.3		
AHY-M			(1) 12.0	(43) 12.6 [0.80] 10.9 14.7	(99) 12.3 [0.73] 10.2 13.8	(35) 12.3 [0.76] 10.3 14.1	(18) 12.3 [0.72] 10.9 13.6	(23) 12.6 [0.69] 11.0 13.7	(18) 13.0 [0.93] 10.5 14.5	(34) 13.5 [1.34] 11.8 15.3	(1) 16.2	
AHY-U	(6) 14.2 [2.00] 11.0 16.6	(2) 13.2 12.7 13.6	(131) 13.3 [1.04] 10.8 17.2	(876) 12.5 [1.00] 9.7 16.9	(289) 11.9 [0.98] 9.4 15.5	(2) 12.8 12.5 13.1	(3) 12.4 11.8 13.2	(38) 12.3 [0.81] 10.8 14.0	(50) 12.6 [0.95] 10.8 14.8	(525) 13.2 [1.06] 10.1 16.7	(57) 13.8 [1.12] 10.1 16.0	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
SY-F				(1) 10.5	(2) 11.8 11.5 12.0			(2) 11.6 10.8 12.3		(4) 13.8 12.8 15.3		
SY-M	(1) 13.5			(1) 12.1	(7) 12.6 [0.74] 11.6 13.6	(1) 12.7			(1) 11.9	(4) 12.6 12.0 14.0		
SY-U	(2) 14.4 14.0 14.8		(1) 10.5	(8) 12.5 [0.52] 11.9 13.5	(8) 11.9 [0.24] 11.5 12.3			(1) 12.4	(1) 12.6	(5) 12.8 [0.83] 11.8 13.6	(1) 12.7	
ASY-F				(4) 12.8 12.2 13.4	(5) 12.5 [1.48] 11.5 15.1			(5) 11.6 [0.81] 10.9 13.0	(3) 12.1 11.8 12.2	(2) 12.6 12.5 12.7		
ASY-M		(1) 13.7	(1) 12.3	(32) 12.2 [0.63] 10.7 13.6	(31) 12.4 [0.53] 11.3 13.5	(4) 12.2 11.8 12.6	(2) 12.5 11.8 13.1	(4) 13.2 12.7 13.5	(6) 12.9 [1.26] 10.7 14.4	(10) 13.1 [0.69] 11.8 14.2		
ASY-U				(8) 12.8 [0.74] 11.6 14.0	(8) 12.1 [1.01] 10.4 13.5				(5) 13.5 [1.25] 11.9 15.0	(8) 12.4 [0.54] 11.8 13.6	(1) 15.0	(1) 14.0
TY-F					(1) 12.3					(1) 11.5		
TY-M				(6) 12.8 [0.67] 12.1 13.7	(3) 12.0 11.6 12.2					(2) 12.7 12.5 12.8		
TY-U				(7) 12.3 [0.64] 11.6 13.5							(1) 13.0	
ATY-F				(1) 13.7	(6) 13.4 [1.55] 11.5 15.6	(1) 13.8	(3) 12.0 11.5 12.5	(4) 11.7 10.2 13.3		(2) 13.7 13.3 14.0		
ATY-M			(1) 13.0	(22) 12.6 [0.92] 11.4 14.8	(20) 12.7 [0.73] 11.5 14.6	(1) 11.9	(3) 12.4 12.3 12.6	(4) 12.5 11.3 13.6	(2) 13.1 12.9 13.3	(5) 12.6 [0.40] 12.2 13.2	(1) 15.3	
ATY-U	(2) 15.3 14.6 15.9		(6) 13.4 [0.81] 12.5 14.8	(8) 12.5 [0.55] 11.3 13.0	(3) 12.0 11.5 12.6			(1) 10.5	(1) 13.7	(8) 13.5 [1.28] 12.2 15.6	(1) 12.7	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-U								(3) 11.2 10.6 12.0	(25) 12.7 [0.92] 10.8 14.7	(261) 13.0 [0.96] 10.0 17.1	(50) 13.6 [0.81] 11.9 15.2	(12) 13.4 [1.37] 10.2 15.0

White-crowned Sparrow

Zonotrichia leucophrys

n = 231

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(1) 27.0	(64) 27.4 [2.64] 18.9 33.1	(4) 30.2 23.1 33.3	
AHY-U					(118) 30.0 [3.22] 24.6 38.5				(3) 25.3 23.1 26.5 33.3	(41) 28.0 [2.56] 21.6 33.3		

White-throated Sparrow

Zonotrichia albicollis

n = 3501

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U									(88) 24.2 [1.65] 19.5 28.2	(1220) 25.5 [2.06] 19.3 32.6	(306) 26.8 [2.74] 20.3 37.1	(3) 27.8 26.3 29.2
AHY-U	(10) 28.2 [3.78] 20.7 34.3	(2) 24.7 24.1 25.3	(20) 26.8 [3.55] 22.2 34.1	(232) 27.7 [2.39] 22.0 35.4	(163) 25.8 [2.45] 21.2 33.7		(1) 29.2		(29) 24.2 [1.36] 22.0 27.9	(1061) 25.7 [2.10] 19.9 33.1	(59) 27.1 [2.35] 19.0 32.2	(1) 28.5
SY-U	(2) 30.1 29.4 30.8	(1) 30.0	(7) 25.8 [2.46] 22.3 28.6	(2) 27.2 26.5 27.8	(1) 23.6							
ASY-U	(1) 32.1		(3) 29.1 28.2 29.6	(1) 28.3								
U-U									(27) 24.4 [1.60] 22.1 29.0	(232) 25.0 [2.02] 19.6 30.8	(23) 26.6 [1.99] 23.5 31.1	(6) 28.8 [2.42] 25.4 31.8

Fox Sparrow

Passerella iliaca

n = 446

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U										(56) 35.2 [2.40] 29.6 40.4	(50) 37.4 [2.78] 32.6 43.9	

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
AHY-U			(141)	(69)	(2)					(37)	(47)	
			36.7	37.4	35.0					35.3	38.4	
			[2.71]	[2.70]	34.0					[2.32]	[3.51]	
			29.4	32.3	36.0					30.5	27.2	
			43.1	47.0						40.0	49.0	
U-U										(17)	(26)	(1)
										35.6	40.3	44.4
										[2.97]	[3.48]	
										32.0	33.3	
										43.6	46.2	

Lincoln's Sparrow

Melospiza lincolnii

n = 845

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(2)	(212)	(268)	(3)	
								17.7	16.6	17.2	20.3	
								17.3	[1.61]	[1.51]	16.3	
								18.0	11.2	11.5	24.6	
									20.6	22.5		
AHY-U					(76)	(2)			(62)	(63)	(1)	
					18.6	17.7			17.2	17.4	17.5	
					[1.82]	17.1			[1.50]	[1.78]		
					14.8	18.3			13.7	11.5		
					24.0				20.1	21.6		
U-U									(101)	(54)		(1)
									16.7	17.2		17.3
									[1.52]	[1.23]		
									10.4	14.8		
									20.3	20.2		

Swamp Sparrow

Melospiza georgiana

n = 2178

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-U								(3)	(105)	(964)	(115)	
								14.8	16.0	16.8	17.4	
								14.2	[1.26]	[1.44]	[1.85]	
								15.4	13.8	11.1	14.0	
									20.0	22.5	22.1	
AHY-F				(1)			(1)					
				19.3			15.8					
AHY-M				(2)	(3)							
				16.8	17.6							
				16.7	16.1							
				16.8	19.0							
AHY-U	(1)	(1)	(8)	(191)	(154)				(12)	(432)	(27)	
	19.6	18.3	17.8	17.1	16.7				15.9	17.2	17.9	
			[2.03]	[1.58]	[1.64]				[1.00]	[1.51]	[1.13]	
			15.1	13.3	12.8				14.4	10.9	16.1	
			21.1	22.2	20.5				17.5	22.0	20.5	
SY-M				(1)	(1)							
				16.5	17.5							
SY-U		(1)		(2)								
		18.9		17.3								
				16.6								
				17.9								

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
U-U									(9) 16.2 [1.17] 14.3 17.6	(140) 16.5 [1.47] 12.4 20.8	(3) 18.0 17.7 18.6	(1) 15.8
Song Sparrow <i>Melospiza melodia</i> n = 5596												
Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
HY-F							(3) 18.6 18.3 19.0	(1) 18.6	(3) 19.6 19.6 19.7	(3) 19.9 18.3 21.1	(1) 21.5	
HY-M							(3) 20.3 20.0 20.7	(3) 20.3 19.3 21.2	(4) 20.6 19.7 21.6	(4) 20.8 19.5 22.4	(7) 20.6 [0.97] 19.6 22.5	
HY-U						(14) 19.5 [1.10]	(141) 19.2 [1.33]	(163) 18.9 [1.33]	(261) 19.6 [1.31]	(1202) 20.4 [1.53]	(208) 21.1 [1.60]	(3) 23.4 22.1 25.0
AHY-F			(4) 19.5 17.1 22.6	(30) 20.9 [1.78] 18.1 25.6	(25) 21.4 [2.14] 17.2 26.1	(11) 20.6 [1.97] 17.2 25.2	(15) 19.6 [1.17] 16.9 22.3	(32) 19.3 [1.83] 11.9 22.4	(14) 20.9 [1.64] 18.1 23.6	(9) 20.4 [0.78] 19.2 21.3		
AHY-M	(1) 22.8	(1) 21.5	(19) 20.6 [1.19]	(43) 20.9 [1.56] 18.3 22.3	(60) 20.6 [1.31] 18.2 23.5	(8) 20.8 [1.31] 18.5 23.2	(8) 20.7 [0.65] 19.4 21.4	(8) 20.1 [0.94] 18.8 21.4	(5) 22.3 [1.95] 20.1 25.3	(6) 21.0 [1.01] 19.2 21.9	(1) 21.4	
AHY-U	(6) 25.0 [1.43] 22.9 27.3	(5) 23.9 [1.96] 21.0 25.9	(1090) 21.6 [2.05] 15.1 27.9	(646) 20.8 [2.03] 11.4 29.1	(27) 20.1 [1.39] 17.4 23.2		(4) 19.9 17.6 23.4	(14) 20.1 [1.71] 18.1 23.0	(18) 19.8 [1.65] 14.3 21.7	(618) 20.8 [1.53] 15.6 28.0	(102) 21.8 [1.48] 18.3 24.9	
SY-F			(7) 20.4 [0.71] 19.3 21.1	(5) 21.2 [0.67] 20.4 22.1	(1) 22.2		(1) 22.5 19.1	(1) 23.5	(1) 20.3 19.2 21.6	(3) 20.3 19.2 21.6		
SY-M	(1) 26.1		(4) 21.3 20.2 23.1	(15) 22.3 [2.37] 19.7 29.8	(8) 20.9 [0.67] 20.3 21.5			(1) 23.1				
SY-U		(1) 24.3	(8) 21.6 [0.60] 20.7 22.5	(3) 19.2 18.5 19.8		(3) 20.3 19.9 20.6		(1) 20.8	(2) 23.9 21.7 26.0	(5) 20.9 [1.01] 20.1 22.4	(2) 21.5 21.3 21.6	
ASY-F				(2) 20.1 19.7 20.4	(2) 20.3 19.8 20.7		(1) 19.7	(2) 18.1 17.6 18.6				

Age/Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ASY-M			(6) 21.8 [1.01] 20.4 23.5	(5) 21.0 [0.80] 20.0 22.0	(1) 20.5			(1) 21.4		(2) 21.8 20.2 23.3		
ASY-U		(1) 28.1	(1) 20.2	(2) 20.2 20.1 20.3					(2) 20.2 19.3 21.1	(2) 20.0 20.0	(1) 24.1	
TY-F				(1) 25.0	(4) 21.1 20.2 22.2							
TY-M			(3) 22.4 21.4 24.2	(1) 22.0				(1) 22.1				
TY-U				(1) 20.0		(1) 23.3						
ATY-F			(2) 20.7 20.0 21.3	(1) 21.2	(1) 22.5							
ATY-M			(3) 22.1 21.0 23.0	(12) 21.3 [1.20] 18.7 22.9	(2) 20.8 20.7 20.8		(1) 23.2	(3) 21.0 19.9 21.6		(3) 20.3 19.3 22.2	(1) 22.7	
U-F									(1) 20.5			
U-M										(1) 20.0	(3) 21.0 20.0 21.8	
U-U							(1) 18.2	(18) 20.5 [1.46] 18.5 22.8	(73) 20.2 [1.31] 16.7 23.0	(430) 20.7 [1.59] 11.7 26.6	(54) 21.2 [2.14] 11.9 24.6	(16) 23.1 [1.58] 20.2 26.2



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BULLETIN

of CARNEGIE MUSEUM OF NATURAL HISTORY



ECOLOGY AND TAXONOMY OF AFRICAN SMALL MAMMALS

Edited by
DUANE A. SCHLITTER

NUMBER 6

PITTSBURGH, 1978

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DUANE A. SCHLITTER
Associate Curator, Section of Mammals

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BULLETIN OF CARNEGIE MUSEUM OF NATURAL HISTORY

Number 6, pages 1-214, 48 figures, 58 tables, 1 appendix

Issued 7 November 1978

Price: \$15.00 a copy

Craig C. Black, *Director*

Editorial Staff: Hugh H. Genoways, *Editor*; Duane A. Schlitter, *Associate Editor*; Stephen L. Williams, *Associate Editor*; Teresa M. Bona, *Technical Assistant*.

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CONTENTS

Editor's Notes — Duane A. Schlitter	9
Evolution of the rump region in the golden-rumped elephant-shrew — Galen B. Rathbun	11
Review of drinking behavior of African fruit bats (Mammalia: Megachiroptera) — Wim Bergmans	20
Ecological position of the family Lorisidae compared to other mammalian families — Pierre Charles-Dominique	26
The identity of <i>Gerbillus bottai</i> Lataste, 1882 (Mammalia: Rodentia), from Sennar, Sudan — Dieter Kock	31
Karyotype of <i>Gerbillus pyramidum</i> I. Geoffroy (Rodentia, Gerbillidae) from Senegal — Bernard Hubert and W. Böhme	38
Karyological and morphological comparisons of <i>Lemniscomys striatus</i> (Linnaeus, 1758) and <i>Lemniscomys bellieri</i> Van der Straeten, 1975, from Ivory Coast (Mammalia: Muridae) — E. Van der Straeten and W. N. Verheyen	41
Revision of the genus <i>Saccostomus</i> (Rodentia, Cricetomyinae), with new morphological and chromosomal data from specimens from the lower Omo Valley, Ethiopia — Bernard Hubert	48
Taxonomic review of the fat mice (genus <i>Steatomys</i>) of West Africa (Mammalia: Rodentia) — Pierre Swanepoel and Duane A. Schlitter	53
A critical examination of alleged sibling species in the lesser three-toed jerboas (subgenus <i>Jaculus</i>) of the North African and Arabian deserts — David L. Harrison	77
Energetics of survival in <i>Heterocephalus glaber</i> (Rüppell), the naked mole-rat (Rodentia: Bathyergidae) — J. U. M. Jarvis	81
Modeling of the population cycles of two rodents in Senegal — Bernard Hubert, F. Adam, and Alain R. Poulet	88
Radio-tracking of a small rodent, <i>Hybomys univittatus</i> , in an African equatorial forest — Huguette Genest-Villard	92
Seasonal population changes in rodents in the Kenya Rift Valley — M. J. Delany and C. J. Roberts	97
Modern rodent fauna of the lower Omo Valley, Ethiopia — Bernard Hubert	109
Evolution of the rodent population of a dry bush savanna in the Senegalese Sahel from 1969 to 1977 — Alain R. Poulet	113
Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari — J. A. J. Nel	118
Notes on the food and foraging behavior of the bat-eared fox, <i>Otocyon megalotis</i> — J. A. J. Nel ..	132
Coexistence in Transvaal Carnivora — I. L. Rautenbach and J. A. J. Nel	138
Systematics of the Hyracoidea: toward a clarification — H. N. Hoeck	146
Patterns of speciation in African mammals — Peter Grubb	152
The Dahomey Gap—a reevaluation of its significance as a faunal barrier to West African high forest mammals — C. Brian Robbins	168
A numerical re-appraisal of the southern African biotic zones — I. L. Rautenbach	175
Karyotypic data for African mammals, with a description of an <i>in vivo</i> bone marrow technique — Lynn W. Robbins and Robert J. Baker	188
Problems and priorities of research on the taxonomy and ecology of African small mammals — Duane A. Schlitter	211

EDITOR'S NOTES

The contents of this volume are the results of some of the scientific reports presented at a colloquium on the ecology and taxonomy of African small mammals hosted by Carnegie Museum of Natural History from 19 to 22 September 1977. In all, forty-one persons who generally specialize in research on African small mammals responded to invitations and met during that period; some presented results of their research during formal morning sessions but, perhaps more importantly, all joined in afternoon discussions centered around an attempt to increase the international cooperation and coordination of research on a continental basis. Such an approach is becoming more important with the increasing cost of research, changing environments and destruction of some ecosystems, and political instability in Africa. Studies of medical zoology in Africa continue to point out the need for continent-wide studies of taxonomy and long-term studies of ecology of potential small mammal hosts of disease vector and reservoirs of causal organisms. Changing weather patterns with protracted droughts, and increasing population growth outstripping food supplies, make it necessary that as little of the resources as possible be lost to small mammal damages. Finally, there has been a tremendous upsurge in interest in African mammals on the part of conservationists, particularly regarding endangered species and the potential extinction of some gene pools.

The state of research on ecology and taxonomy of small mammals in Africa is a number of decades behind that of Europe and North America. The contents of this volume will amply indicate the differences in approach to solving the various problems and the general "state of the art" in this area of research. Only through cooperation and coordination of research efforts can the highest return be obtained.

Because of limited logistical support and facilities, the number of participants invited to this colloquium was kept low. If another is scheduled in the near future, perhaps wider participation among specialists will be possible.

Individual papers in this volume have been arranged in generally accepted phylogenetic order regardless of topic, beginning with elephant shrews and continuing through hyraxes. Near the end are the papers dealing with speciation and biogeography; these are followed by a review of published

karyological data for African mammals. The final paper discusses problems and priorities of research on the taxonomy and ecology of African small mammals. From an editorial standpoint, an attempt was made to get as much uniformity of style as possible without significantly changing the context of the manuscripts.

The completion and publication of this volume would not have been possible without the unselfish support, cooperation, and encouragement of Hugh H. Genoways, Publications Editor, Carnegie Museum of Natural History. I am deeply indebted to him for all of this help. My thanks go also to Teresa M. Bona, Technical Assistant for Publications, who was helpful beyond the requirements of her job in retyping, editing, and checking of manuscripts, and in keeping records and addresses; Stephen L. Williams, Associate Editor, for working with the figures; and Nancy Perkins for enhancing some of the figures. My warmest thanks must go to the individual contributors for their cooperation and support in putting together this volume.

The colloquium which precipitated this volume would not have been possible without the active support of a number of people. Chief among these are the people who helped house and feed the participants and furnished transportation to the colloquium site. Suzanne Braun, Cathy H. Carter, Murray H. de la Fuente, Stefannie B. Elkins, Hugh H. Genoways, Joyce Genoways, Caroline A. Heppenshall, Mary Ann Jones, Thomas J. McIntyre, Suzanne McLaren, R. Laurie Robbins, Judith Schlitter, Pierre Swanepoel, Daniel F. Williams, and Stephen L. Williams all helped in many ways. Mary H. Clench, Albert O. and Gilbert O. Lenhart, and Dan Roslund worked hard to assure that the colloquium site was satisfactory. I want to thank William and Ingrid Rea and Graham and Jane Netting for offering sleeping quarters for a number of the participants. The Market Spot, Bud's Bakery, Valley Dairy, Goodman's Distributing Co., and William Downs, Penn State University Southwestern Regional Experimental Farm, helped assure that all were well fed. Ruth Scott and Martha Shope allowed us the use of various personal items of furniture. William Campbell, Carnegie Institute Cafeteria, was helpful in acquiring various items. Ann R. Nieser and Flora Gibson typed many invitations and proposals. I am grateful for the help and support of all of them.

A portion of the travel support of some of the participants from Africa was made possible by a grant from the Office of International Programs, National Science Foundation (INT77-08721).

Whatever success this colloquium enjoyed is directly related to the support of Craig C. Black, Director of Carnegie Museum of Natural History. Although the idea for such a colloquium was formulated in 1972, it was not possible to begin serious planning until 1976. At this time, Dr. Black pledged his support and helped make it financially

possible to have such a colloquium and to publish a volume of proceedings resulting from it.

Finally, I want to thank Karl F. Koopman of the American Museum of Natural History, New York, for serving as Honorary Chairman. I am grateful that he would lend his support to the idea of a colloquium. During the colloquium he freely offered the stability and knowledge gained by his years of experience to insure that an atmosphere of professionalism was maintained throughout the meeting.

DUANE A. SCHLITTER

EVOLUTION OF THE RUMP REGION IN THE GOLDEN-RUMPED ELEPHANT-SHREW

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ABSTRACT

Rhynchocyon chrysopygus has a distinct rump patch, which lies just above an area of exceptionally thick skin ("dermal shield"). The possible function(s) of these structures are discussed in relation to published hypotheses for the evolution of other mammalian rump patches and dermal shields. It is sug-

gested that conspecific territorial aggression and diurnal predation have resulted in the two structures evolving both as a morphologically protective conspecific target organ and a pursuit invitation signal.

INTRODUCTION

The literature dealing with the function of mammalian rump patches not only contains several different hypotheses for their evolution, but also, in some cases, attempts to explain the occurrence of nearly all mammalian rump patches with one model (Smythe, 1970a; Guthrie, 1971). In this paper I will consider some of these hypotheses in terms of life-history data from an elephant-shrew (Macroscelideidae), which suggests that some rump patches have evolved due to more than one selection process and serve multiple functions. In the development of the multifactor hypothesis, it should become clear that it is unrealistic to apply any one explanation for the evolution of rump patches to all mammalian taxa.

The golden-rumped elephant-shrew, *Rhynchocyon chrysopygus* Günther, is restricted to the open forests and woodlands of coastal Kenya north of

Mombasa. It is the largest elephant-shrew species, weighing about 540 g and having a head-body length of about 280 mm (Fig. 1).

I began a 21-month field study of free-living *R. chrysopygus* at the Gedi Historical Monument (20 km south of Malindi) in April 1971. The 44-ha monument is covered with lowland, semi-deciduous forest with a 20-m high canopy. The forest floor is relatively open and covered with a carpet of dead leaf litter throughout the year (Fig. 2).

Animals were driven into fishing nets strung loosely along the ground. Each individual was fitted with a distinct combination of colored bird bands on its rear legs before being released. Behavior of marked animals was studied by systematically walking a trail grid through the forest.

RESULTS AND DISCUSSION

Life History

R. chrysopygus is diurnal, spending nearly 75% of the day slowly walking along the surface of the forest floor noisily probing for invertebrates with its long nose and forefeet (Fig. 2). It neither climbs nor burrows, but is capable of very swift cursorial locomotion. During the night it sleeps in a dry leaf nest on the forest floor. The individuals of monogamous pairs occupy equal, congruent territories (mean 1.7 ha) which they defend sex-specifically. Territorial defense involves linear chases, one animal running behind another, until the intruder is driven over a boundary. The long canine teeth of

adults are probably associated with this aggression. Pair-bond behaviors are infrequent, yet the pair is stable over time, changing only when an individual disappears. The animals breed continuously throughout the year. Adult coloration is exhibited at birth by the single, precocial young weighing about 80 g. It is weaned when it first emerges from the nest, about 2 weeks after birth. It then follows its mother around for 2 or 3 days before becoming almost completely independent on the parental territory. There is no parent-young aggression and subsequent offspring may simultaneously occupy the parental territory.



Fig. 1.—Adult *Rhynchocyon chrysopygus*, illustrating the distinct golden rump patch.

The southern-banded harrier hawk (*Cicaetus fasciolatus*), black mamba (*Dendroaspis polylepis*), cobras (*Naja* spp.), and man are known predators. The elephant-shrew's reaction to potential predators is very similar to many ungulates (Eisenberg and Lockhart, 1972). It freezes at the first sign of danger, but if further disturbed, walks slowly away, loudly slapping its tail on the dead leaf litter; or it runs away in a gait that is like that of a stotting gazelle; or it flees at full speed, loudly hammering the leaf litter with its rear legs. In all cases it normally stops just within sight of the predator, and pauses until the latter makes another move. Then it either takes flight again or, after 5 to 15 min, silently disappears into the forest. If two or more individuals are disturbed, they flee in different directions. Once established on a territory, *R. chrysopygus* may live to be 3 or 4 years of age. The life history of this elephant-shrew is documented in more detail in my dissertation (1976) and monograph (in press).

During the behavioral work I collected monthly specimens for reproductive and diet studies. This material was taken from the nearby, structurally similar Arabuko-Sokoke Forest, in an area which was scheduled for clear-cut and burning. While preparing study skins from these specimens, differences in skin thickness were noticed. On several skins the subdermal muscles were carefully removed and then a grid was inked on the inner surface of the fresh, flat skins. Thickness was measured with a screw-gauge micrometer. Hair lengths were measured from randomly chosen hairs cut from the surface of study skins.

The Rump Patch

Both sexes have a distinct golden rump patch, which is only slightly erected when the animals are excited or stressed. There is no difference in the extent of rump patch coverage between the sexes. Rump hair is longer than hair on the middle of the back (means = 22.2 mm and 16.6 mm, respectively;



Fig. 2.—Predator's view of a foraging adult *Rhynchocyon chrysopygus* on the open, leaf-littered forest floor at Gedi Ruins.

20 specimens, 15 hairs each). The rump hair length of females is significantly longer than that of males (means = 23.0 mm and 21.4 mm, respectively; 10 specimens each, 15 hairs/specimen; $P < 0.001$, t-test). The 1.6 mm difference between the means is so small that it is doubtful whether it has any appreciable visual effect. This is especially true when considered in relation to the overlap between the range of mean rump hair lengths for the different individual female and male specimens (20.4 mm–27.2 mm and 19.1 mm–24.2 mm, respectively).

The Dermal Thickening

In both sexes the skin under the rump patch is thicker than on the middle of the back (Figs. 3 and 4). This is most pronounced in males. One normal adult male specimen had rump skin that was three times thicker than on the back. Histological examination of an adult male's rump skin shows that there are no unusual features except for its thickness (Fig. 5). Subadult animals do not show dermal thickening. It is probable that the shorter rump hair

in males is a secondary effect of their thicker rump skin. If hair length could be measured from follicle tip to hair tip, there probably would be no significant difference in length between the sexes.

When all visible, small body scars from 84 study skins are cumulatively plotted on a skin-map, they all fall on or very near the rump patch (Fig. 6). Male skins have proportionally, but not significantly, more scars than females ($P < 0.5$, χ^2 test). I think the most likely explanation is that these scars result from canine wounds inflicted during intraspecific aggressive chases.

Sexual Dimorphism and Sex-Specific Behavior

The only externally visible sexual dimorphism is the much longer male canine tooth. Ten adult female and 10 adult male specimens had significantly different canine lengths (Table 1; see Ansell and Ansell, 1973, for a similar condition in *Rhynchocyon cirnei*).

There is evidence that males were more intensely

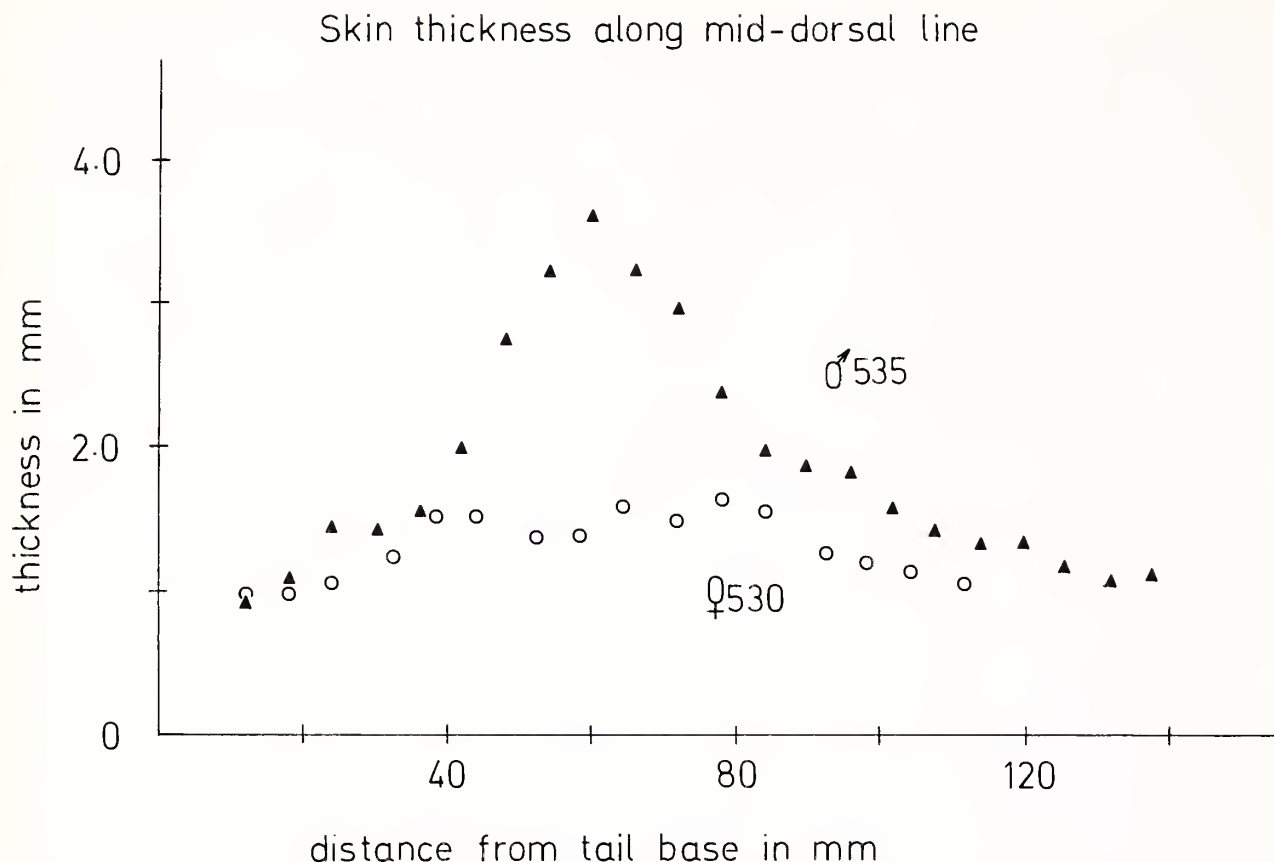


Fig. 3.—Skin thickness of an adult male and female *Rhynchocyon chrysopygus*.

territorial than females, for they scent marked, “violated” territorial boundaries, and were involved in interpair aggressive encounters more frequently than females (Table 1). Aggressive encoun-

ters were infrequent events, but in a 1 week period I saw the same two females chase one another many times, which is very unusual. These data contribute to the lack of significance between the levels of male and female aggression in Table 1.

Table 1.—Sexual dimorphism and sex specific behaviors in *Rhynchocyon chrysopygus*.

Trait	Female	Male	Chi-square on original data
Mean canine length	4.6 mm	6.6 mm	$P < .001$
Scent marking*	3.3%	9.7%	$P < .001$
Territorial violations*	3.1%	12.2%	$P < .001$
Interpair aggressive encounters*	1.0%	1.3%	$P < .5$

* % of total sightings.

Hypotheses for the Evolution of Dermal Thickening

If dermal thickenings function as protective shields from dense vegetation, as proposed by Dubost and Terrade (1970) in the chevrotain, *Hymoschus aquaticus*, and in duikers, *Cephalophus* spp., then some substantial difference in behavior between the sexes would be expected to explain the sexually dimorphic thickening. This reasoning also applies to the idea that dermal thickenings may serve as a protective device against predators. No differences in behavior were observed that would support either of these two hypotheses for *R. chrysopygus*.

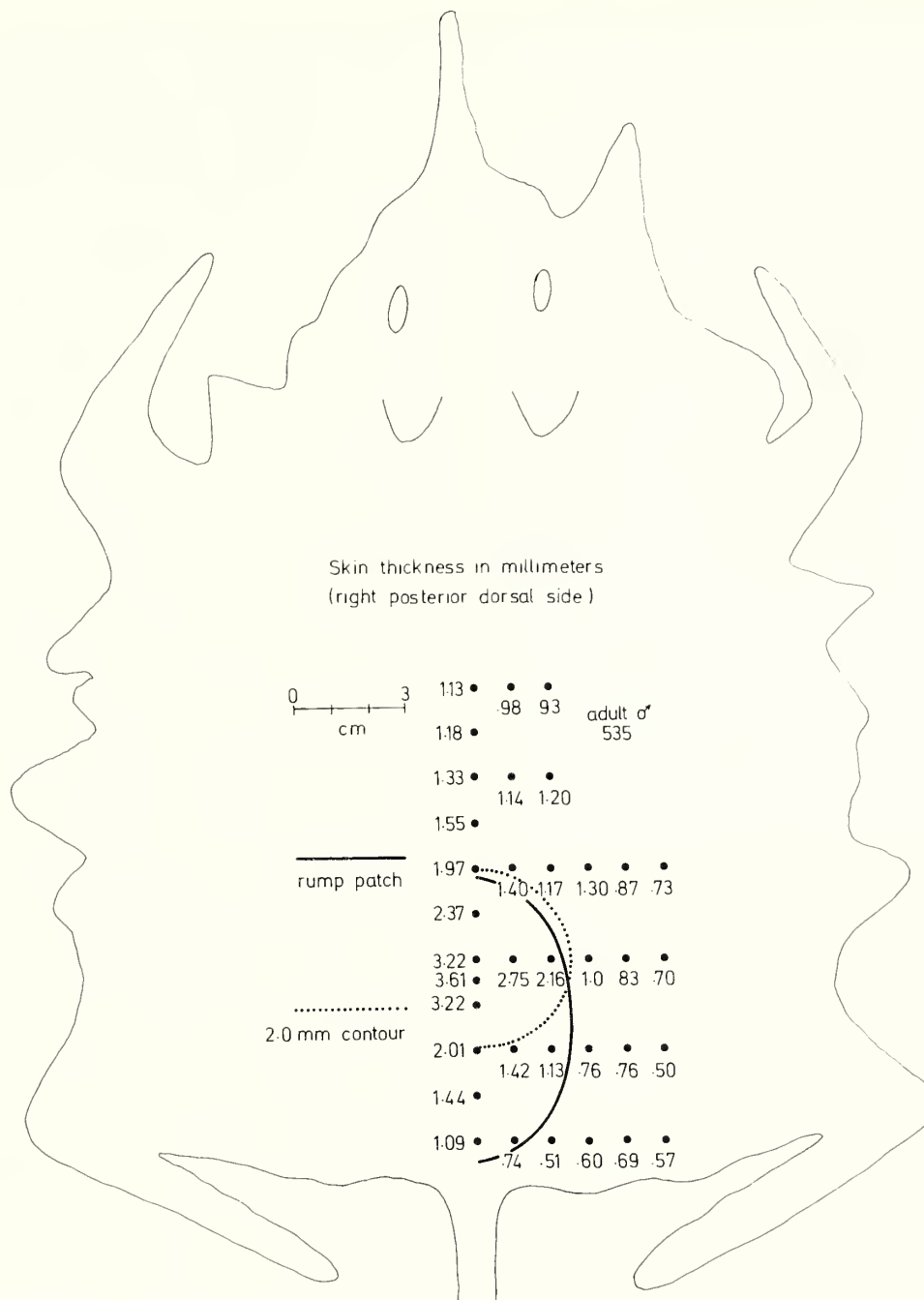


Fig. 4.—Skin thickness and rump patch location on an adult male *Rhynchocyon chrysopygus*. Solid-line arc represents rump patch margin, dotted-line arc the 2.0 mm thickness contour of the dermal shield.

It has been suggested that thick rump skin may serve, in some way, to erect the rump patch. The male rump patch does not appear any more or less erectile than the female's, and there is no histological evidence for such a mechanism in the skin (Fig. 5).

The mountain goat, *Oreamnos americanus*, is described by Geist (1967) as having a "dermal shield" where injury would most likely occur during conspecific fighting. Jarman (1972) found a similar structure in the territorial impala, *Aepyceros melampus*. Perhaps *R. chrysopygus* has evolved a

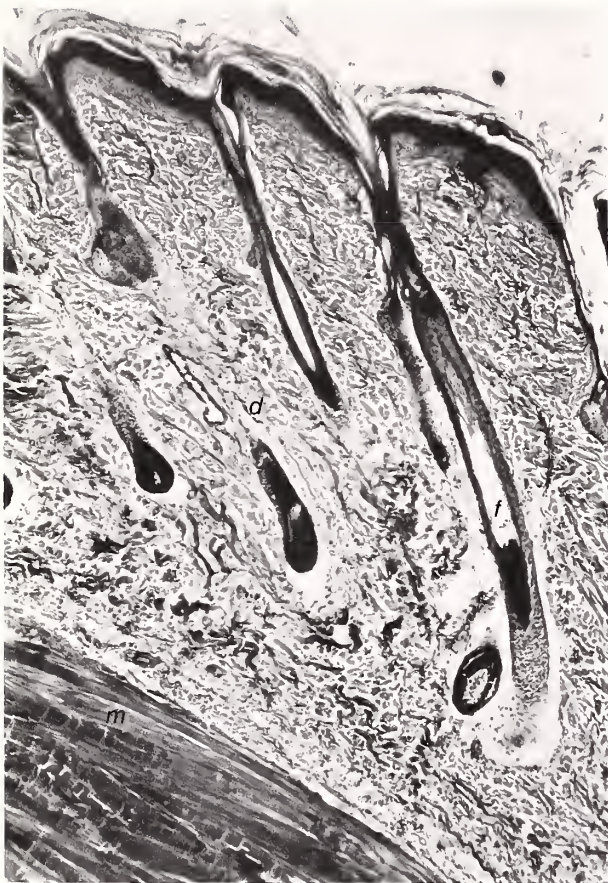


Fig. 5.—Longitudinal section of rump skin from an adult male *Rhynchocyon chrysopygus*. m = subdermal muscle. f = hair follicle. d = dermis.

dermal shield in response to territorial interpair aggression. This hypothesis is supported by the elephant-shrew's large canine tooth, fighting behavior, dermal shield location, cumulative scar pattern, and the thicker shield in the more intensely territorial male.

Hypotheses for the Evolution of the Rump Patch

Guthrie (1971), stimulated by Geist's ideas (1971) on mountain sheep (*Ovis canadensis*), proposed that mammalian rump patches evolved as intraspecific appeasement or submission signals. These signals function by changing a dominant animal's aggression to a sexual behavior due to the rump region's association with copulatory displays. Guthrie (1971) also suggests that other rump patch functions may be secondarily derived from the original submission/appeasement function. Kleiman

(1974) suggests that the various rump displays in the hystricomorph rodents have secondarily evolved different functions from the original sexual function. I never observed any specific elephant-shrew rump patch display behavior that would support Guthrie's ideas for *R. chrysopygus*. In this elephant-shrew, the process of redirecting aggressive behaviors to sexual behaviors by a rump patch display would presumably not function in female-female encounters because a rump display would not stimulate a female sexually. This would result in only males evolving the rump patch, which is not the case in *R. chrysopygus*.

It has been suggested that a rump patch may increase the golden-rumped elephant-shrew's crypsis in the patchily-lighted, dry-leaf littered forest floor. It is my experience that the animals are not visually or behaviorally camouflaged. Their dark bodies contrast greatly with the light rump patch and leaf litter (Fig. 2), and the elephant-shrew's fleeing behavior does not indicate that it is relying on crypsis as a defense mechanism against detection by potential predators.

There is little evidence to support the hypothesis that *R. chrysopygus*'s golden rump functions as an intraspecific predator warning signal, as proposed for the rump patch of fallow deer, *Dama dama* (Alvarez et al., 1976). *R. chrysopygus* pairs were only rarely within visual contact of each other (less than 20% of my sightings) and because the rump patch is not highly erectile, there is no distinct on/off mechanism, which would be necessary if it were to function in this manner. There is some evidence that the tail slapping and rear-leg hammering behaviors can serve as warning signals (Rathbun, in press).

It has been suggested that the elephant-shrew's rump patch is a visual cohesive signal between the newly emergent young and a parent, helping to maintain a close distance between a pair while they forage. This function would be the visual equivalent of the auditory stridulating organ in the tenrec (*Hemicentetes semispinosus*; Eisenberg and Gould, 1970). The juvenile cohesive signal function is not consistent with the lack of a father-juvenile bond and the presence of a rump patch in male *R. chrysopygus*.

Hirth and McCullough (1977) present data to support an antipredator cohesive signal function for the tail-flagging display of the white-tailed deer, *Odocoileus virginianus*. In this case, the individuals of the prey species benefit by a coordinated flight from

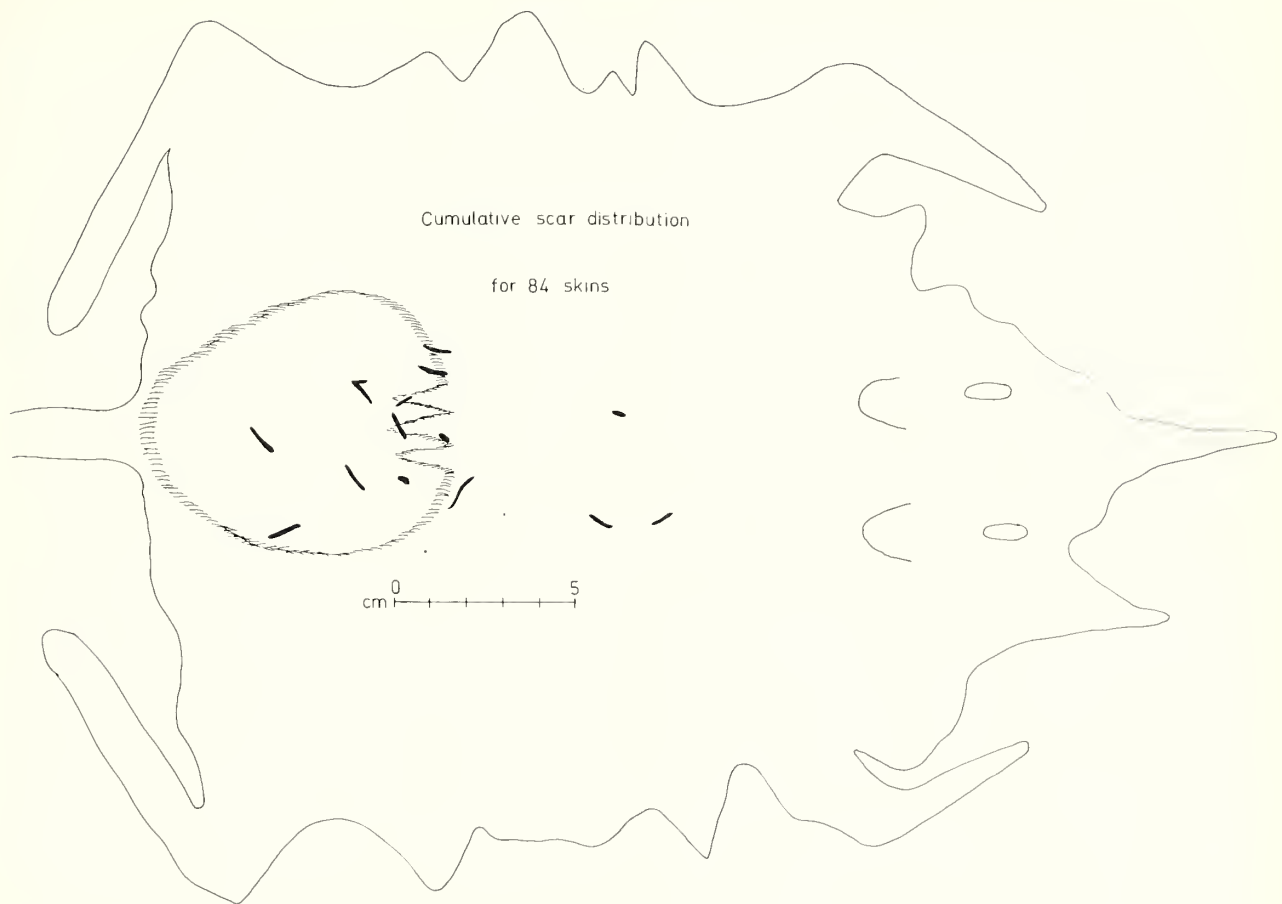


Fig. 6.—Location of 13 dermal scars (five female and eight male) from 43 female and 41 male *Rhynchocyon chrysopygus* study skins.

a predator, which is signalled by the rump display. The dispersed nature of the elephant-shrews, together with their flight in different directions when disturbed, does not support the antipredator cohesive signal function for the golden rump of *R. chrysopygus*.

Smythe (1970a, 1977) suggests that rump patches may serve as predator "pursuit invitation signals." By stimulating a predator to attack prematurely, a healthy individual is able to flee successfully and the location and intent of the predator are revealed, thereby reducing the danger of ambush. Smythe (1970a) suggests that stotting-like gaits and rump patch displays are used to invite pursuit. *R. chrysopygus* is probably frequently preyed upon by the harrier hawk, which hunts visually by perching 2 to 4 m above the relatively open forest floor waiting for an opportunity to make a quick, concealed ambush (Rathbun, in press). This is precisely the type

of predation needed for visual invitation signals to evolve. The structure of the Kenyan coastal forest results in direct-line visibility being restricted to about 10 m, which is conducive to the evolution of auditory invitation signals. I believe the golden-rumped elephant-shrew's rump patch and behavioral complex of stotting, rear leg hammering, tail slapping, and short, obvious flight followed by a pause, are directed toward diurnal bird and mammal predators in an attempt to attract their attention and induce their exposure and/or premature attack, as proposed by Smythe (1970a, 1977).

The three allopatric species of *Rhynchocyon* occupy similar habitats, and except for distinctly different body coloration, their morphology is very similar (Corbet and Hanks, 1968). Kingdon (1974) has suggested several explanations for the variation in color. He thinks the checkered back and rump of *R. cirnei* may be an adaptation for camouflage,

whereas the difference between *Rhynchocyon petersi*, with its pure black back and rump, and *R. chrysopygus* may be related to differences in sexual behavior which evolved as an "ethological barrier." More information is needed on the ecology and behavior of the *Rhynchocyon* species in order to verify these ideas.

I have discussed briefly some hypotheses which might conceivably explain the evolution of the dermal shield and the rump patch in *R. chrysopygus* as though the two structures were unrelated in this animal. The dermal shield lies directly beneath the rump patch (Fig. 4) and I feel that there

is probably an integrated function in the two structures. The rump patch may serve as a conspecific target organ, attracting the blows of a pursuing elephant-shrew to a region of the body, which is not only relatively immune to serious injury, but also morphologically adapted to receive the blows. This is a similar mechanism to the "deflective marks" extensively described by Cott (1940), where a predator is attracted to a less vital part of the body by a very distinctive coloration or marking. In the case of the elephant-shrew, the predator is a conspecific individual defending its territory through aggression and the distinctive mark is the golden rump.

CONCLUSIONS

I think the data for *R. chrysopygus* support a multifactor explanation for the evolution of its rump patch. The location of the dermal shield, the scarring pattern, and the aggressive behavior indicate that the rump patch, with its very distinctive coloration, may serve as a conspecific target organ. On the other hand, because there is no significant sexual dimorphism in the rump patch corresponding with the rump skin, this suggests that the patch may have an additional, even distinct, function. The elephant-shrew's attention-gathering behavior while fleeing a potential predator, and its distinct rump patch, support Smythe's predator pursuit invitation hypothesis (1970a, 1977). Predator selection pressure probably acts equally on both sexes, resulting in the male and female rump patches being equal in size. Thus two distinct selection pressures, conspecific territorial aggression and diurnal predation, are probably involved in the evolution of the rump patch in *R. chrysopygus*.

It is unlikely that the dual rump patch function proposed for the elephant-shrew can be used as a general model for mammalian rump patch evolu-

tion. It is inappropriate to try to apply models developed for relatively social animals, such as many of the larger ungulates (Hirth and McCullough, 1977), to less social species. It would, however, be interesting to compare mammals that have similar life histories, such as *R. chrysopygus* and an agouti, *Dasyprocta*. The latter inhabit South American forests, and, like *R. chrysopygus*, are diurnal, cursorial, territorial, probably monogamous, and some bear a distinct rump patch (Morris, 1962; Smythe, 1970b). The yellow-back duiker, *Cephalophus silvicultor*, may also be comparable to *R. chrysopygus*.

If the rump patch functions proposed above for the golden-rumped elephant-shrew are valid, and Geist (1971), Alvarez et al. (1976), and Hirth and McCullough (1977) are correct in their interpretation of rump patch function in the species that they consider, it would not only seem fairly certain that rump patches have evolved independently several times within the Mammalia (Guthrie, 1971), but probably also due to several different selection pressures.

ACKNOWLEDGMENTS

I am grateful for the support of the National Geographic Society, East African Wildlife Society, and the National Museums of Kenya. Mr. Kashuru Mumba and his family greatly assisted in the collection of specimens. Drs. H. Croze, P. Jarman, H. Kruuk, and A. Walker offered stimulating ideas and direction to the rump patch region aspects of the elephant-shrew project,

which was undertaken as part of a Doctor of Philosophy program in the Department of Zoology, University of Nairobi, Nairobi, Kenya. The participants of the colloquium as well as Dr. Devra Kleiman and Ms. Carolyn Dorsey generously offered helpful comments on drafts of this paper. The National Zoological Park kindly supported my participation in the colloquium.

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REVIEW OF DRINKING BEHAVIOR OF AFRICAN FRUIT BATS (MAMMALIA: MEGACHIROPTERA)

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ABSTRACT

Certain captive African Megachiroptera drink regularly from a hanging posture. There are very few reports of these animals drinking in the wild, nearly all claiming that they would drink by skimming over open water surfaces and scooping water or wetting their fur and licking water from this afterward. This paper

summarizes and critically deals with the literature on the subject, and presents some new evidence suggesting that the skimming maneuvers of some fruit bats might serve a purpose other than drinking. The discussion includes some related observations on Australasian Megachiroptera.

INTRODUCTION

Little has been written about possible drinking habits of African Megachiroptera in the wild. About fruit bats in general Novick (*in* Novick and Leen, 1969) wrote: "Fruit bats like the flying foxes and their smaller relatives rarely drink water, apparently they derive all the water they need from their moist food." Rosevear (1965) stated about West African fruit bats that "the demand of the body for water must be satisfied . . . to a considerable extent by the intake of liquified fruit pulp or floral nectar." Indeed one might expect that these animals, whose diet probably consists mainly of juicy fruits and equally water-rich nectar, would not

need to drink water too. There are reports however which suggest that at least some wild fruit bats do drink. Two ways of drinking have been described, the first for captive animals and the second for animals in the wild. Quite a few species of Megachiroptera have been kept in captivity, but hardly any author paid attention to whether or not his animals drank. Notwithstanding discussions of their diet, it may not even be stated if water was offered (for example, Blackwell, 1966, 1967; Brosset, 1966a; Coe, 1976; Jones, 1972; Lawrence and Novick, 1963).

DRINKING RECORDS

Kulzer (1958, 1969) related how his captive *Rousettus aegyptiacus* (Geoffroy, 1810) and *Eidolon helvum* (Kerr, 1792) drank water from bowls, rapidly with their tongues, in a dog-like manner. *Rousettus* came down to the cage floor to drink, but *Eidolon* preferred to remain hanging. This is most probably related to the ability of *Rousettus aegyptiacus* to take flight from an even surface without effort, as I have observed in the zoo in Amsterdam where a small number of unknown provenance is kept (1977), and the apparent lack of this ability in *Eidolon* (Kulzer, 1968). At Windhoek, Namibia, Dr. C. G. Coetzee kept a crippled specimen of *Eidolon helvum*, which drank regularly from a bowl (personal communication, 20 September 1977.) Brosset (1966b) observed wild *Eidolon helvum*, probably in

northeast Gabon, drinking from the sap of palm trees, which had been collected by Africans for the production of palm wine. As far as I know this is the only record of wild African Megachiroptera drinking in a manner more or less comparable to that observed by Kulzer (1958, 1969) in his captive specimens.

The other manner of drinking described for some Megachiroptera is to skim close to the surface of water and, in some way or other, take in water. In 1841, Prof. J. A. Wahlberg observed unidentified fruit bats near Port Natal (=Durban), South Africa, drinking in this way (Petermann, 1858). Rousselot (1950) related how he saw *Eidolon helvum* and *Epomophorus gambianus* (Ogilby, 1835) flying so close to the surface of a river that they could wet

their ventral fur from which they would lick the water afterward. He observed *Eidolon* doing so at Ségou in Mali, and observed *Epomophorus gambianus* both at Ségou and at Maradi in Niger but does not state where he saw this species perform in this manner. Rosevear (1965) suggested that insectivorous bats would exhibit this behavior much more often than fruit bats would, but does not seem to have observed fruit bats drinking in this way himself. Novick (*in* Novick and Leen, 1969) mentioned the habit for insectivorous bats but, as appears from the above quotation, remained equally vague about fruit bats on this point. The ornithologist Mr. Roy Parker, at the time Curator of the Zoology Museum of the University of Ibadan, Nigeria, told me that

he had often seen how *Eidolon helvum* came down at dusk to the water of the swimming pool of the Staff Members Club on the campus of the university. He believed the animals to be drinking (personal communication, August 1976). Dr. M. El Rayah saw *Eidolon helvum* skimming over the water of the Nile at Khartoum in Sudan, but did not observe further details (personal communication, 20 September 1977). At Makokou, northeast Gabon, Mr. J. Bradbury kept *Hypsignathus monstrosus* Allen, 1861, in captivity in a large enclosure with a large bowl of water on the floor. This bat regularly drank by scooping water with its mouth while flying low over the bowl (Dr. P. Charles-Dominique, personal communication, 20 September 1977).

PADDLING BATS

When traveling through Nigeria in the summer of 1976 I stayed for 2 weeks in Pandam Wildlife Park, a small game reserve just north of the village of Pandam (9°15'N, 7°50'E) that includes the 2 square mile Lake Pandam. There I enjoyed the hospitality of the zoologists Chris Smeenk and his wife Nellie, who told me of their observations of *Eidolon helvum* skimming over the lake. According to them, *Eidolon* did not drink when close to the water surface but touched it with its legs. On 7 July 1976, the three of us made a canoe trip on the lake for a more detailed study of this phenomenon. At twilight, from approximately 1840 to 1920 h, hundreds of *Eidolon* approached the lake, all coming from the southwest and eventually continuing roughly to the northeast. Only a few bats continued their flight without interruption. Most of them, when they had reached open water (much of the lake was covered with water lilies), came down to it in one circular movement (infrequently two or three circles were described). Then they flew parallel with and very close to the water surface for a short time and at a certain moment dipped their hind legs into the water. This dipping lasted much less than a second. Thereafter they flew up and continued on their way. A striking detail was the apparent hesitation, which most bats showed in their movements before dipping. We observed several individuals, who at the last moment refrained from dipping and continued

on their way without having dipped. However, we also saw a small number of bats who dipped more than one time. These continued flying low over the water after their first dip, and dipped up to four times. On one occasion I counted five dips. These repeated dips followed shortly upon one another, reminding one of a well flinched drake-stone. After that these bats also resumed their flight, undoubtedly towards their feeding grounds.

The bats flew in small groups of a few dozens or less, arriving at different times during about 40 min, and all these groups displayed the described behavior. This enabled us to focus on new individuals and observe this behavior many times. Nevertheless, it was very hard to establish what was actually happening. The bats kept considerable distance, apparently avoiding our presence. It proved moreover very difficult to observe correctly what was happening at the division of air and water, and of course our sight was hindered by the gradual fading of light.

Later I heard of a possibly similar observation. The zoologist Rob Robelus told me that he had watched large bats skimming over the water of a swimming pool at Bébédjia near Moundou, in southwest Tchad, in September 1969. These bats touched the water with some part of their ventral side, but were not believed to be drinking (Dr. R. A. Robelus, personal communication, July 1977).

DISCUSSION AND CONCLUSIONS

The more conventional and seemingly more likely way of drinking as described for certain African

Megachiroptera, that is, lapping while in a hanging or clinging position, has been observed in the wild

only once (Brosset, 1966b). Because in this case, the bats (*Eidolon helvum*) drank no water but the probably tasty sap of a palm tree, the question remains whether they were hunger- or thirst-induced. The habit shown by captive *Rousettus aegyptiacus* and *Eidolon helvum* of drinking water regularly does not necessarily reflect natural behavior. Their demand for water may well have been brought about by a shortage of liquid in the food offered. Kulzer (1958, 1969) gave his *Rousettus* bananas, apples, and oatmeal porridge, and his *Eidolon* bananas and figs. In this respect, it is possibly of significance that his *Rousettus* always drank immediately upon feeding (Kulzer, 1958). On the other hand, *Rousettus aegyptiacus* in the Amsterdam zoo, which are given a much more varied diet with juicier fruits, also drink regularly (Mr. F. Gangel, personal communication, August 1977). The fact that wild African Megachiroptera drink regularly, and in a similar manner, is still to be proven.

The other manner of drinking water, by scooping or lapping it directly while skimming close to the water surface or indirectly by wetting the fur while skimming over the water and licking water from the fur afterward, has so far been ascribed to three African species—*Epomophorus gambianus*, *Eidolon helvum*, and *Hypsignathus monstrosus* (Rousselot, 1950; Parker, personal communication, 1976; Charles-Dominique, personal communication, 1977). The first observation, of unidentified species, was made by Prof. J. A. Wahlberg in 1841 near Port Natal, South Africa. The first part of his account reads (in translation): "Port Natal, October 5th, 1841 . . . Some time ago I shot two species of *Pteropus*, one of which I think may be new (possibly a new genus); it has four upper and five lower cheek teeth." Thereafter he relates how he shot them: in the evening over a spring where they came to drink while flying low over the water (*in* Petermann, 1858). Unfortunately he does not mention the name of the species he knew, which would have given a clue to the identity of the other, supposedly new species. Of the fruit bat species now known to occur there, only *Eidolon helvum* and *Rousettus aegyptiacus* had been described at the time of Wahlberg's writing. Kock's assumption (1969) that an *Epomophorus* species was involved here is probably based on the fact that the holotype of *Epomophorus wahlbergi* (Sundevall, 1846) had been collected by Wahlberg near Port Natal. However, this happened 2 years after Wahlberg's observation and shooting of skimming bats, namely on 27 No-

vember 1843 (Andersen, 1912). Moreover, it is clear from Wahlberg's report that his observation applied to both "species" shot by him, one of which he knew (thus probably *Eidolon* or *Rousettus*), and one of which was new to him and which had four upper cheek teeth instead of three as in *Epomophorus*. To my knowledge, cases of additional upper cheek teeth have not been described for this genus (compare the footnote in Andersen, 1912:516). I think, therefore, that Wahlberg had before him a subadult specimen of *Eidolon helvum* or of *Rousettus aegyptiacus* with unerupted M^2 and M_3 . Wahlberg's bat collection, now in the Naturhistoriska Riksmuseet in Stockholm, did not contain other Megachiroptera than the just mentioned holotype of *Epomophorus wahlbergi* (Dr. C. Edelstam, letters of 1 April 1976 and 12 September 1977), although it is not impossible that part of his material was lost, as were many of his original notes (Petermann, 1858).

Precise accounts of what African Megachiroptera actually do when skimming over water are very few. In three cases, they are reported to drink somehow directly (Wahlberg, *in* Petermann, 1858; Parker, this paper; Bradbury, this paper). On two occasions, they were seen to dip with some ventral part of their bodies and definitely not with their snouts (Rousselot, 1950; Robelus, this paper), while one of these observers reported that they lick water from their fur afterward (Rousselot, 1950). On yet another occasion three observers saw *Eidolon helvum* dipping with its legs (this paper).

Wahlberg went to the spring where he saw the skimming bats to shoot them in the first place. Moreover he had fires lit at the sides of the spring to enable him to shoot bats coming near the fire, because otherwise he could not hit them. When looking past these fires at the skimming bats, his chances to observe accurately can hardly have been great, to say the least. I know that Parker made his observations without binoculars, while the bats were skimming the water of a scarcely illuminated swimming pool, and he himself was seated at some distance on a well-illuminated terrace. Again, the circumstances were rather poor. Rousselot's paragraph (1950) dealing with skimming *Eidolon* at Ségou is worth quoting (in translation): ". . . they fly very low over the water and only wet the fur of their breast and belly. Having risen immediately thereafter for two or three meters, they lick this wet fur, simultaneously interrupting their flying movements. Then they rise to make up for the lost height

and lick again. This happens three or four times, after which they repeat the whole maneuver, until they are satisfied." He wrote that *Epomophorus gambianus* acted in the same way, but where he observed this is not stated. With regard to *Eidolon*, it looks very much like Rousselot may have seen what my companions and I saw at Lake Pandam in Nigeria, in which case the aberrant details in his story could be due to careless observation and interpretation. We observed a flying height of at most 30 to 50 cm. Most of the bats we followed dipped (their legs) only one time, some up to four or five times, and they touched the water each time they were near it (we actually saw the splashes). Their movements down to the water were active and deliberate. We observed no interruptions of wing movements, but of course, the bats had to brake their flight in order to descend. We did not see individuals flying more than one stretch at the reported height.

All in all, the evidence that certain wild African Megachiroptera skim over open water surfaces in order to drink is meager and, in part, doubtful. Of course, it is easily conceivable that at least some species do drink water under certain conditions. Forest species might lap water from small reservoirs of different types, such as holes in trees, but populations inhabiting the dryer savanna regions may have to search for larger bodies of water, such as lakes and streams. This may be true for *Eidolon helvum* in particular, because this species roosts exposed to the sun, unlike other African Megachiroptera, and may need extra water to make up for its potentially stronger transpiration. However, why should they drink by means of the seemingly hazardous skimming maneuvers instead of getting at the water through climbing down to it along tree branches? This latter behavior has been reported for wild specimens of an unidentified *Pteropus* species from Sumatra (van Balen, 1914). Ratcliffe (1961) saw flying foxes (most probably species of *Pteropus*) drinking by the skim-and-scoop method in New South Wales on the Nambucca River in 1930, and offshore on Bougainville, Solomon Islands, in 1945. He tried to explain this by assuming that these bats were drinking salt (or salty) water for the sake of mineral salts, which their normal food would not supply in adequate quantities. His observations on the Bougainville bats reminded me of our own of *Eidolon* at Lake Pandam. He also emphasized the importance of focusing on individual bats to obtain an idea of what they were doing.

He observed large groups of bats flying to the sea just after sunset. Each bat would cruise up and down for a while, and then fly right down to the sea once or twice (some three times) and then leave the flying mob and head inland, presumably to set out on its nightly food search. If the water was calm enough, he and his co-observer did see the actual lap-splashes. From the latter remark in his account, it is clear that it must have been very difficult to see (after sunset) whether the bats were scooping water or wetting their fur or dipping their legs. Another interesting report is that of Mr. J. V. de Bruijn (*in* Ripley, 1960), who at the north coast of New Guinea observed large flying foxes trying to pick up fruits, which were floating on the sea surface just offshore. Ratcliffe (1961) thought that these bats may also have been drinking salt water instead of picking up fruits. I do not know of other reports on Megachiroptera outside Africa skimming over water in order to drink. There must be more, because in a popular account on Indonesian flying foxes van Bemmelen (1974) wrote (in translation): "Their habit of scooping water while flying low over its surface is well-known." The salt-water story does not hold for the fresh-water skimming African bats, and in general I doubt whether Ratcliffe's conclusion is correct. Many fruit bats will never have an opportunity to drink sea water, and quite a few, apparently, skim over fresh water. Moreover, the wild Sumatran *Pteropus* mentioned by van Balen (1914) drank fresh water, albeit from a hanging posture, and captive *Pteropus giganteus* (Brünnich, 1782) are reported to "drink often, especially during the summer" (Sányál, 1892).

The question remains why *Eidolon*, at least on one well-documented occasion, dipped its legs. One can think of several explanations, none of which seems good enough. *Rousettus aegyptiacus* in the Amsterdam zoo not only drinks from its water bowl, but also uses it to take baths. A freshly bathed bat licks itself and is licked by the others (Mr. F. Gangel, personal communication, August 1977). This could hardly be a way of drinking, as the animals also drink "normally." Could it be a means to clean the body, maybe even of certain parasites, or could it have some thermoregulatory function? If one of these questions would eventually produce a satisfying explanation with regard to *Rousettus*, would this explanation also satisfy us with regard to the wild, leg-dipping *Eidolon*? I do not think so. In this regard, *Eidolon helvum* is easy to study, as it roosts in large numbers and fully

exposed near many human settlements. It is known that *Eidolon* passes its day, like so many other mammals, partly with grooming its body and fur. It is also sufficiently known that common external parasites of *Eidolon*, such as the nycteribiid fly, *Cyclopodia greeffi* Karsch, and the spintumicid mite, *Meristaspis* sp. (Adecsun, 1974), have no preference whatsoever for the legs or lower abdomen of their hosts. Moreover these parasites attach themselves so firmly to the skin of the bat that a little water will not harm them in the least. Likewise, a thermoregulatory purpose of the wetting of so small a part of the body is hard to understand.

Another possibility is that the water itself does not play the important role, which we have tried to attach to it. Could *Eidolon* be picking something out of the water (as there were, on Lake Pandam, hardly any fruits, these can be disregarded)? Could *Eidolon* possibly be fishing? Carnivorous behavior has recently been reported of two other African Megachiroptera. Van Deusen (1968) cited someone, who observed wild *Hypsignathus monstrosus* pick up and eat the skinned bodies of birds, which had been tossed outside a house, and also how it attacked live chickens near the same house, at M'Bigou in Gabon. Coe (1976) kept *Lissonycteris angolensis* (Bocage, 1898) in a cage together with *Myonycteris torquata* (Dobson, 1878), at Mount Nimba, Liberia, and saw how specimens of the former species actually attacked and devoured specimens of the latter. It is of interest to quote here (in translation) the report on a Sumatran *Pteropus* by van Balen to which I referred before in relation to its drinking behavior. "My son Mr. D. J. van Balen, living at Serbadjadi (Galang), Deli, observed that kalongs (=flying foxes) do drink. He used to spend the night now and then on a platform in a forest tree to watch animals. One night he saw a number of flying foxes alight in a dead tree, climb down along branches which hang over the water of a deep pool, and drink while hanging from these branches. After drinking they let themselves fall onto the surface of the water, where they stayed for some moments, constantly flapping their wings, and then flew up in the limited space in circular movements until they could take flight in the open air above the trees." This observation was repeated on request, and I think it should be taken seriously. Later, van Balen's son was told by a native that the flying foxes did not descend to the pool to drink, but to catch the little fishes which abounded in such pools. Dr. F. A. Jentink, the well-known Dutch

mammalogist, wrote to van Balen that he did not believe that kalongs drank, and he warned him against native stories. But why then, asked van Balen, would kalongs perform such breakneck stunts? (van Balen, 1914).

Apparently this belief in fishing kalongs is more widespread (though not so much in the literature), as van Bemmél (1974) also mentioned it (and rejected it). Apart from the hint at possible piscivorous behavior of *Pteropus* van Balen's account (1914) deals with another aspect of the relation between Megachiroptera and water. It confirms that they, or at least certain *Pteropus* species, can swim. Ryberg (1947) cited Trouessart's story on how, during James Cook's second journey around the world (1772-1775), swimming Megachiroptera were observed in the Tonga Archipelago. These were probably *Pteropus tonganus* Quoy & Gaimard, 1830. Some of the fruit bats seen picking up fruits from the sea surface in North New Guinea (Ripley, 1960) "dipped too far into the water, became caught and splashed in. The instant this happened, the flying foxes came to rest quietly on the surface with wings well spread. Thence they gradually rode in on the waves of the rising tide. The sea was not too rough, and gradually they tumbled into the light surf and quickly proceeded to drag themselves out of the wave area. Without exception, the bats then crawled up the beaches, occasionally shaking themselves, and made for the low dunes above high water mark." Beyond these dunes the bats climbed up small trees and launched themselves into the air again. Novick and Leen (1969) gave a splendid series of photographs of a swimming *Pteropus giganteus* (Brünnich), but unfortunately it is not stated where they were taken. Van Bemmél (1974) knew of a *Pteropus* kept as a pet on a houseboat on Sumatra. This animal once fell into the water. Thereafter, it made a daily habit of plunging into the water and swimming about for a while (until, 2 years later, it was seized by a crocodile).

Summarizing, it has not yet been sufficiently documented that, in the wild, African Megachiroptera need to drink water. In captivity *Rousettus aegyptiacus* and *Eidolon helvum* may drink from bowls, and *Hypsignathus monstrosus* is reported to drink through the skim-and-scoop method. In the wild *Eidolon helvum* and *Epomophorus gambianus* have been seen to skim over open water, but none of the reports in which they would do so in order to drink seem to stem from really careful observation. The behavior of captive *Hypsignathus monstrosus* and

of many wild Microchiroptera supports the idea that physically Megachiroptera may be able to drink while skimming. *Eidolon helvum* has been seen to skim over open water not to drink but to dip its legs for an unknown purpose. Of skimming and swimming Australasian species of the genus *Pteropus* (which in its ecology and ethology shows a great resemblance to *Eidolon*) it has been suggested that they might be fishing, and as carnivorous behavior has been reported for some African fruit bats, I do

not exclude fishing as a possible explanation for the leg-dipping of *Eidolon*. Against this would be that *Eidolon* is also attracted by swimming pools, but I do not suggest that drinking as one of the possible aims of skimming Megachiroptera should be neglected. More critical observation in the wild, and possibly some experimenting with captive fruit bats (large enclosures with large, fish-inhabited water containers on the floor; small, whole fishes as part of their diet) should provide the final answers.

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ECOLOGICAL POSITION OF THE FAMILY LORISIDAE COMPARED TO OTHER MAMMALIAN FAMILIES

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ABSTRACT

African primates of the family Lorisidae are compared to other families of African mammals from the perspective of ecological niche occupancy. It is shown that lorisids, along with other rodents and carnivores, occupy an ecological niche characterized

by arboreal-nocturnal-climbers and/or leapers-animalivores-frugivores-gumivores habits (A.N.C.L.A.F.G.). Generally, mammals (especially primates and carnivores) occupying this type of niche exhibit many primitive evolutionary characters.

INTRODUCTION

Among primates, Strepsirhini (Afro-Asian and Madagascan lemurs) represent 18% of the living species. In terms of their anatomy, physiology, and behavior, they are considered more primitive than the "higher primates" (Catarrhini and Platyrrhini). Although five Malagasy families (of which two are subfossils) are the result of a radiative evolution, the Cheirogaleidae and the Lorisidae (in Africa and South Asia) have retained numerous primitive features (Charles-Dominique and Martin, 1970). The taxonomic position of these two groups have been discussed by different authors (Cartmill, 1975; Charles-Dominique and Martin, 1970; Charles-Dominique, 1977; Goodman, 1975; Hoffstetter, 1974, 1977; Martin, 1972; Pocock, 1918; Simpson, 1945; Szalay and Katz, 1973; Szalay, 1975; Tattersall and Schwartz, 1975; Van Kampen, 1905; Van

Valen, 1969; Weber, 1928). According to the interpretation of early primate history by each author, the Lorisidae and Cheirogaleidae have been classified either in two different suborders, two different families, or two different subfamilies. Nevertheless, even if the Cheirogaleidae and the Lorisidae have been geographically separated since the early Tertiary, they share numerous characters inherited from a common ancestor, and presently occupy similar ecological niches.

In this paper, the ecological position of one of these two primitive families (Lorisidae) and its relationship to other mammalian groups living in the same forest ecosystem are discussed. Different ecological parameters shall be analyzed including diet, activity rhythms (nocturnality or diurnality), habitat preference, and locomotor patterns.

FOOD PROVIDING ENERGY AND FOOD CONCERNED WITH THE RESTORATION OF TISSUES

It is necessary to make a distinction between food which is used for energy (glucids) and food which balances the loss due to tissue turnover (for example, loss of proteins, see Hladik, 1977).

Food providing energy.—Every molecule catabolized by an organism can be used for energy. For example, strict carnivores and strict insectivores (= "animalivores") use glucids, lipids, and proteins for energy. Proteins are difficult to find in large quantities and many animals eat small quantities of proteins necessary for their balance, but use lipids and especially glucids as energetic food. Soluble glucids (C5, C6, and C12 sugars) are directly assimilable by a nonspecialized gut. They are found in

fruits like berries, drupes, and so on (especially in fruits with a fleshy pericarp around the stone). Non-soluble glucids (celluloses, hemicelluloses, and others) are made up of soluble sugars polymerized in complex chains. Mammalian enzymes cannot break these long chains, but they are hydrolyzed by bacteria in specialized digestive ducts (stomach of ruminants, sacculated stomach, caecum). Celluloses and hemicelluloses are the principal constituents of leaves and wood. Gums are produced by some trees and lianas after different actions (insect bites, xylophages, other injuries). Composed of C5 and C6 sugars polymerized in long chains, they are biodegraded in the caecum by bacteria (for Prosimians).

Food concerned with the restoration of tissue.—

In addition to vitamins and mineral elements, which are generally present in sufficient quantities in natural food, amino acids (associated in proteins) play a major role in the constitution of the tissues (turnover, growth, gestation, and lactation). In the forest, proteins can be found in prey, in kernels, and in the green part of plants (especially young shoots). These three sources are correlated with different specializations: prey capture is correlated with morphological and behavioral specializations of preda-

tors; kernel and seed intake is correlated with dental specializations allowing opening of hard stones, and gut specializations for detoxification of secondary compounds often present in seeds; leaf intake is correlated with the specialization of the digestive duct. This last solution, generally used by animals which can digest the cellulose, requires large quantities of bulky food relatively poor in assimilable proteins.

As "energetic food," proteins can be a limiting factor for animal populations.

NOCTURNALITY AND DIURNALITY

Theoretically, food resources are available around the clock but consumers are generally specialized to feed during either the day or night (Charles-Dominique, 1975). It seems that among higher vertebrates, birds are specialized to the diurnal way of life and mammals to the nocturnal. Of course, secondary specializations allow some birds to feed during the night and some mammals to feed during the day, but they are limited. For example, in the Gabon forest, 70% of the mammals are nocturnal, 10% are nocturnal and diurnal, and 20% are strictly diurnal (among 120 species of mammals); in the same ecosystem, 96% of the 216 bird species are diurnal. The same picture exists in the tropical forest of Panama where 86% of the mammals are

nocturnal, 6% nocturnal and diurnal, and 8% strictly diurnal (Eisenberg and Thorington, 1973). The diurnal mammals compete successfully in four different ways, which can be listed as follows: increase in body size (monkeys, apes, antelopes, and big carnivores); continually growing incisors (a system which enables squirrels to open tough fruits and nuts); claws to dig out hidden prey (some squirrels, Callitrichidae monkeys, and some anteaters); development of intelligence (especially for monkeys).

In terms of competition for food, it is necessary to separate the "nocturnal world" from the "diurnal world."

ECOLOGICAL POSITION OF THE FAMILY LORISIDAE

Lorisids (10 species of which there are eight in Africa) are all arboreal, nocturnal animals. They find proteins by hunting prey; the energetic food is found mainly in soluble sugars (soft fruits) and/or in gums which are biodegraded in the caecum. Secondary specializations allow several species to live sympatrically, avoiding competition for food. For example, five species of Lorisidae live in the same ecosystem of the rain forest in Gabon (two loraginaes = slow-moving climber animals and three galaginaes = fast-running and leaping animals). The two Lorisinae (*Arctocebus calabarensis* and *Perodicticus potto*) are specialized in the capture of irritant and pungent-smelling prey ignored by the three Galaginae species (*Galago elegantulus*, *G. alleni*, and *G. demidovii*). *A. calabarensis* live in the understory, in recent tree-fall zones and *P. potto* in the canopy. An equivalent separation exists

among the three galaginaes—*G. elegantulus* live in the canopy where they feed on insects and gums; *G. alleni* live in the undergrowth and feed on insects and fruits; *G. demidovii*, the dwarf bushbaby, hunt prey (70% of their diet) in thick vegetation composed of a mixture of lianas and tree foliage (Charles-Dominique, 1971, 1977). *A. calabarensis* and *G. demidovii* are the two smallest species of their respective subfamilies. They succeed in feeding almost entirely on prey (85% and 70%). The three other much larger species capture the same absolute quantities of prey but they must complement this food by fruits and/or gums (food providing energy).

The ecological niches of the Lorisidae can be defined as Arboreal-Nocturnal-Climbers and/or Leapers-Animalivores-Frugivores-Gumivores (=A.N.C.L.A.F.G.).

DIRECT COMPETITORS OF THE LORISIDAE

The Lorisidae are not the only mammals to occupy such ecological niches (A.N.C.L.A.F.G.); in Gabon, the Paradoxurinae *Nandinia binotata* (palm civet) and several rodents can be found in them: *Graphiurus murinus* (Gliridae), and *Thamnomys rutilans*, *Praomys tulbergi*, *Praomys lukolelae*, *Stochomys longicaudatus*, *Hylomyscus stella*, *Hylomyscus fumosus*, *Hylomyscus aeta*, and *Hylomyscus parvus* (Muridae).

With the exception of *Graphiurus murinus* and *Thamnomys rutilans*, which are true arboreal animals, these species generally live at a lower level of the forest but can interfere with lorises in the undergrowth. Because of a poor knowledge of their ecology, an estimate of the total number of A.N.C.L.A.F.G. mammals is between eight and 15 species. In addition, other categories of sympatric mammals whose diet can interfere with those of A.N.C.L.A.F.G. mammals must be considered (for example, some bats which hunt prey hidden in the foliage).

The more complex the forest, the more different biotopes and, thus, different ecological niches it presents. In Gabon, where the forest is one of the most complex in the world (1,000 to 2,000 species of trees and lianas) eight to 15 mammal species occupy these A.N.C.L.A.F.G. ecological niches (among 120 sympatric mammalian species). In comparison, the dry forest of the west coast of Madagascar (Morondava region) is composed of about 150 species of trees and lianas; only five species of mammals (four primates—*Microcebus murinus*, *Microcebus coquereli*, *Cheirogaleus medius*, and *Phaner furcifer*—one rodent—*Eliurus* sp.) occupy the A.N.C.L.A.F.G. ecological niches among 19 sympatric mammalian species. In South Africa and East Africa, gallery forest and woodland-savanas are poor in species of trees and lianas (about 100 species per ecosystem); only one species of Lorisidae, or rarely two (*Galago senegalensis* and/or *Galago crassicaudatus*), can be found in these ecosystems (Bearder, 1974; Bearder and Doyle, 1974).

Population densities change as a function of the abundance of arboreal mammalian species in relation to the complexity of the forest. In Gabon, if we consider the five lorisid species together, they

form an overall population of about 160 individuals/square km. In South Africa and East Africa, the population of *Galago senegalensis* and/or *Galago crassicaudatus* is generally more abundant—110, 112, 125, 175, 183, 200, 175, 500 individuals/square km according to the area (Bearder, 1974). In the dry forest of western Madagascar, the four primate species, ecologically equivalent to the Lorisidae (Cheirogaleidae) form an overall population of about 500 individuals/square km (Charles-Dominique and Petter, 1978).

At first sight, in spite of the scarcity of plant and animal species, the animal populations of dry forests are highly concentrated (Table 1). In fact, for an ecosystem we must consider all the species occupying the A.N.C.L.A.F.G. ecological niches. In Gabon, the Lorisidae constitute only five of the eight to 15 mammalian species adapted to these niches; the bushbabies in South Africa and the Cheirogaleidae in western Madagascar are practically the only species to occupy homologous ecological niches in their respective ecosystems. At the present time, it is impossible to make an evaluation in Gabon, but it is probable that the overall density of the eight to 15 Gabonese species living in A.N.C.L.A.F.G. niches (or at least their biomass) is roughly equivalent to those calculated for their relatives in dry forests.

In the Gabon rain forest ecosystem, the different families which occupy similar niches of the A.N.C.L.A.F.G. categories avoid food competition by developing some morphological, ethological, and physiological specializations, in the same manner as the different lorisid species avoid food competition. These specializations are differences in body weight (rodents—10 to 50 g; lorises—60 to 1,000 g; palm civet—2,000 to 4,000 g, and prey capture techniques (prey size is generally related to predator size).

Bushbabies detect prey by vision and hearing. Capture is achieved by a rapid stereotyped movement of the hand, often when the insect is flying or ready to escape (Charles-Dominique, 1971, 1977). This elaborate system provides the bushbabies with exclusive access to some categories of mobile prey living in the foliage.

CONCLUSION—DISCUSSION

If animals which are phylogenetically as different as the primates, rodents, and carnivores discussed in

this paper can occupy ecological niches of the A.N.C.L.A.F.G. types (Arboreal, Nocturnal,

Table 1.—Comparative situations of A.N.C.L.A.F.G. (=Arboreal, Nocturnal, Climber/Leaper, Animalivore-Frugivore-Gumivore) lemurs (*Lorisidae* in Africa, *Cheirogaleidae* in Madagascar) and sympatric mammals in three different ecosystems—Gabon, rain forest of Makokou area; South Africa, different gallery forest and wooden savannas of Transvaal, Zululand, and eastern Rhodesia; Madagascar, West Coast, Morondava area. Even with a higher number of species, the lemurs of the rain forest occur in lower population densities compared to dry forest species. This low value, in rain forests, can be related to the presence of numerous other mammalian competitors living in sympatry (A.N.C.L.A.F.G. mammals).

Parameters	Gabon rain forest	South Africa dry forest	Madagascar dry forest
Number of plant species (trees—shrubs—lianas)	1,000–2,000	#100	#150
Number of sympatric mammals	120	?	20
Number of sympatric arboreal mammals	38	10–15	8
Number of sympatric A.N.C.L.A.F.G. mammals	8–15	#5	#5
Number of sympatric A.N.C.L.A.F.G. lemurs	5	1–2	4
Total density of sympatric A.N.C.L.A.F.G.* lemurs (square km)	160	110–500	600

Climber/Leaper, Animalivore-Frugivore-Gumivore), it is probably because these modes of life do not require such complex specializations as animals exploiting areas or food of “difficult” access. In South America, the didelphid marsupials of the genera *Marmosa*, *Philander*, and *Caluromys*, which present numerous primitive characters, also occupy similar ecological niches. The Jurassic panthotherian (140 million years old) found in Portugal is considered to have been insectivorous and arboreal in habits (Buffetant, 1977) probably close to those observed for the above species.

One can consider that these modes of life were adopted very early by different primitive mammals which, later, could give rise (or not) to taxa ecologically adapted to other types of life.

Among strepsirhines (African and Malagasy lemurs) the two families presenting the greatest number of primitive characters—*Lorisidae* and *Cheirogaleidae*—occupy ecological niches of the A.N.C.L.A.F.G. type. The situation is identical to that of *Paradoxurinae* (palm civets) as compared to other subfamilies of *Viverridae*. These A.N.C.L.A.F.G. ecological niches can be considered as “conservative”; they are not related to major modifications of the primitive mammalian model. Among *Muridae*, most of which are terrestrial or semiterrestrial animals, some species have been able to colonize these ecological niches without developing particular adaptations.

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THE IDENTITY OF *GERBILLUS BOTTAI* LATASTE, 1882 (MAMMALIA: RODENTIA), FROM SENNAR, SUDAN

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ABSTRACT

Two recently collected gerbils from the Gezira, Sudan, are identified as *Gerbillus bottai* Lataste 1882. They are compared with other species of the subgenus *Hendecapleura* (*campestris*, *c. wassifi*, *nanus*, *n. garamantis*, *pusillus*, *harwoodi*, *watersi*, and *henleyi jordanii*) and discussed with further described taxa (*stigmatomys*, *luteolus*, *venustus*). The proposal is made to con-

sider *G. stigmatomys* as a *nomen dubium*, and to unite *G. luteolus* and *G. harwoodi* under the older name *G. bottai*.

The use of the geographical name Sennar is briefly explained for a more careful consideration in connection with restrictions of type localities and animal distribution.

INTRODUCTION

During an investigation of harmful rodents in the Sennar region of the Sudan, Mr. Arno H. Hoppe of the Deutsche Gesellschaft Für Technische Zusammenarbeit (GTZ) collected several specimens of small mammals, which were sent for identification to the Forschungsinstitut Senckenberg, Frankfurt a.M. Among the specimens received were *Crocidura s. sericea* (Sundevall 1843) from Fadasi Halimab (Southern Gezira Dist.), *Crocidura flavescens*

hedenborgiana (Sundevall 1843) from Ma'tuq (Dueim Dist.), *Arvicanthis abyssinicus* (Ruppell 1942) from Fadasi Halimab and Wad Medani, *Mastomys natalensis macrolepis* (Sundevall 1943) from Wad Medani and Barakat (Southern Gezira Dist.), *Taterillus gyas* Thomas 1918 and *Acomys dimidiatus* (Cretzschmar 1826) from Gadambalia (Gedaref Dist.), and two gerbils discussed below.

SYSTEMATIC DISCUSSION

Gerbillus (*Hendecapleura*) *bottai* Lataste, 1882

Specimens examined.—Bageir = El Bageir, Northern Gezira Dist., Blue Nile Prov., 15°21'N, 32°45'E, 1♀ (skin, skull) SMF 50158; Managil, Southern Gezira Dist., Blue Nile Prov., 14°15'N, 32°58'E, 1♀ (skin, skull) SMF 50159.

Comparative material of the subgenus Hendecapleura Lataste 1882.—*G. campestris* LeVaillant, 1857: S. W. Matmata, S. Tunisia, 2♀ (2 skins, 2 skulls) SMF 52328, 52329; El Goléa, Algeria, 1 sex unknown (skin, skull) SMF 51629; Imlaoulaouen, Hoggar, Algeria, 1♂ (skin, skull) SMF 51630; Guelta Afilale, Hoggar, Algeria, 1♂, 4 sex unknown (5 skins, 5 skulls) SMF 51631–51635. *G. campestris wassifi* Setzer, 1958: Bahig, Western Desert, Egypt, 2♂, 1♀ (3 skins, 3 skulls) SMF 26804–26806. *G. n. nanus* Blanford, 1875, Rafsanjan, Kerman Prov., Iran, 1♀, 3♂ (4 skins, 4 skulls) SMF 46370–46372, 46374. *G. n. garamantis* Lataste, 1881: Oued Noun, S. E. Goulimine, S. Morocco, 7♂, 2♀ (7 skins, 2 alc., 9 skulls) SMF 47676–47684. *G. stigmatomys* Heuglin, 1887: Jebelein, E. bank White Nile, Blue Nile Prov., Sudan, 1♀ (skin, skull broken) AMNH 82219. *G. pusillus* Peters, 1878: Iraka, Tanzania, 2♀ juvenile (2 alc., 1 skull) SMF 11494, 11495. *G. harwoodi* Thomas, 1901: Mt. Suswa, Rift Valley, Kenya, 10 sex unknown (broken skulls from owl pellets) SMF 41513–41519, 41527, 41530–41531; S. shore L. Naivasha, Kenya, 1♀ juvenile (alc., skull) SMF 42297 [This species averages larger (most obvious in M¹-M³) than the sympatric *G. pusillus* (Petter, 1975; Roche 1976)]. *G. watersi* DeWinton, 1901: Shendi, Northern Prov., Sudan, 2♂ (2 skins, 2 skulls) B.M. 1.5.5.55, 1.5.5.56 (para-

types). [Listed by Petter (1975) as a valid species and as a subspecies of *G. nanus*, said to occur in Upper Nile, Sudan, which places it in the southern Sudan. The occurrence of a subspecies of *nanus* in the horn of Africa besides *watersi* (Petter, 1975; Roche, 1976) hints to the specific validity of *watersi*.] *G. henleyi jordanii* Thomas, 1918: Gabès, Tunisia, 1♂, 1♀ (2 skins, 2 skulls) SMF 19543, 19544; Jebel Mrhila, Tunisia, 2♀ (2 alc., 1 skull) SMF 28598, 29599.

Lataste (1882a) recognized the new species *G. bottai* (two skulls, one skin from Sennar, collected by Botta in 1834) among misidentified gerbils and had already used the new name in a session of the Société Zoologique de France on 13 December 1881 in explaining the synonymy of *Gerbillus gerbillus* Olivier, 1801 (Lataste, 1882b), but the original description was not published until 1 March 1882 (Lataste, 1882c).

This description is based on two skulls and one skin with incomplete tail; the latter nearly unicolored, dorsal coloration not clearly set off from ventral side; hind feet naked, shorter than in *G. quadrimaculatus* Lataste, 1882, from Nubia, a supposed synonym of *G. campestris* LeVaillant, 1857. The two skulls were both 25 mm long (which is probably

Table 1.—External and cranial measurements of selected specimens of the genus *Gerbillus*.

Measurements	Holo- type <i>G.</i> <i>boitai</i> Lataste, 1882c	B.M.21.- 4.18.6 juv. Sennar		SMF		Holo- type <i>G.</i> <i>luteolus</i>		AMNH		Holo- type <i>G.</i> <i>harwoodi</i>		SMF 41513-9, 27, 30, 31 Rift Valley
		Setzer, 1956	Present study	El Bageir	SMF 50158 ♀	SMF 50159 ♀	Managil	type <i>G.</i> <i>stigma-</i> <i>monyx</i>	82219 <i>G. stig-</i> <i>monyx</i>	<i>G. stigma-</i> <i>monyx</i>		
										♂	♀	
Head and body length	85	—	—	86	85	95	90	87	—	82	—	—
Tail length	[62]	—	—	107	93	110	93	104	—	113	—	—
Hind foot length	20	—	—	21	22	23	21	20	—	22	—	—
Ear length	6	—	—	11	11	12	—	—	—	10	—	—
Greatest length of skull	25	22.7	22.6	26.5	26.3	28	—	27.3	26.5	26	—	—
Condylbasal length	—	19.6	20.6	24.0	24.3	—	—	24.8	23.6	—	—	—
Basilar length	—	—	—	22.0	21.9	21	—	—	—	19	—	—
Mastoid breadth	—	—	—	11.7	11.3	—	—	—	—	—	—	—
Braincase breadth	—	—	11.0	12.1	11.8	12.2	—	13.5	13.6	12	—	—
Zygomatic breadth	—	—	—	14.1	13.7	14.0	—	14.2	14.2	—	—	—
Interorbital breadth	—	4.2	4.0	4.8	4.5	4.8	4.4	4.9	4.9	4.5	—	4.3-4.8; M = 4.5; N = 7
M ¹ -M ¹ breadth, crown	—	—	4.9	5.4	4.9	—	5.5	—	—	—	—	5.0-5.2; M = 5.1; N = 3
M ¹ -M ¹ breadth, alveolar	—	—	4.2	4.9	4.7	—	4.7	—	—	—	—	4.7-4.9; M = 4.8; N = 4
Diastema length	—	—	5.2	6.7	6.8	7.2	7.0	—	—	6.5	—	5.8-6.4; M = 6.2; N = 9
For. incisiv. length	—	3.8	4.0	4.3	4.3	4.7	4.5	4.9	4.7	5	—	4.3-4.8; M = 4.7; N = 9
Nasal length	—	7.8	7.4	9.7	8.6	10	9.9	9.9	9.8	10	—	—
Bullae length	—	7.4	6.2	9.4	9.7	—	9.6	9.4	9.4	—	—	—
Mandible angular	—	—	—	12.9	12.8	—	12.8	—	—	—	—	—
Mandible condylar	—	—	—	13.7	13.8	—	13.6	—	—	—	—	—
M ¹ -M ³ crown	}	3.8	3.5	3.6	3.5	3.6	3.5	3.7	3.8	3.6	—	3.40-3.83; M = 3.60; N = 9
M ¹ -M ³ alveolar		—	—	4.1	3.7	—	4.2	—	—	—	—	3.75-4.20; M = 3.92; N = 9
M ¹ -M ₃ crown	—	—	—	3.5	3.4	—	—	—	—	—	—	—
M ¹ -M ₃ alveolar	—	—	—	3.6	3.6	—	—	—	—	—	—	—
M ¹ breadth	—	—	1.3	1.3	1.3	—	1.25	—	—	—	—	1.20-1.38; M = 1.30; N = 10

the total occipital-nasal length) and nearly as large as in *G. quadrimaculatus*, that is, somewhat shorter; posterior border of interparietal bone salient in the middle, which instead of being concave, is a transversal rhomboid with rounded corners; incisors less strongly colored, the molars heavier than in *G. quadrimaculatus*.

G. bottai differed from *G. garamantis* by narrower posterior region of the skull, less inflated bullae, and lighter molars. In *G. garamantis*, the interparietal bone is concave, foramen incisivum remains well away from the molars, and the palatine foramina start from the first tubercle, not from the following lamina of M^1 as in *G. bottai*. The remaining comparisons were made with forms of the subgenus *Gerbillus*.

In the course of a series of papers, Lataste included *bottai* in the new subgenus *Endecapleura* Lataste, 1882d (later emended to *Hendecapleura* by himself) with a question mark only, together with *garamantis* Lataste, 1881 (genotype), *nanus* Blandford and possibly *Quadrinacutatus* (sic) Lataste, 1882.

The two new specimens now under discussion agree well in size with the original description of *bottai* (Table 1), but not in the form of the interparietal bone, the situation of the incisive and palatine foramina, and separation of coloration between dorsal and ventral side.

However, *G. garamantis* from southern Morocco also does not fit the comparison given by Lataste (1882c). Because of the missing tail tip in the only skin of *G. bottai*, nothing is known about the form of the tuft.

The two new specimens have tails longer than the head and body (Table 1), slightly darker above, with a weakly developed tail tuft, dorsal and ventral color clearly separated; clear white postorbital and auricular spots; hind foot relatively broad, middle finger not elongated and approximately one-fourth of the total hind foot length; and a few short hairs scattered on the distal part of the hind foot.

Nothing was said of the deposition of the original material; Thomas (1919) noted that the specimens were not in the Lataste collection received at the British Museum, but confirmed DeWinton (1901) that *G. bottai* was based on specimens in the Paris Museum. However, Rode (1945) did not list *G. bottai* among the type specimens of Gerbillinae.

There are apparently only two specimens of *G. bottai* available for study in the British Museum; these were examined by Setzer (1956). One of them

was collected by S. S. Flower (B.M. 21.4.18.6, skin and skull of a juvenile) at Sennar, Blue Nile, and the older one (B.M. 46.6.2.44, skin in poor condition), by Hendenborg in Sennar, was received in exchange from the Stockholm Museum by Sundevall. Without a doubt, these specimens, one younger and the other older than the original description, could have been identified only by comparison with the description.

One of the recent specimens (SMF 50158) was sent to the British Museum for direct comparison with the two unique *G. bottai* (Table 1). The results (including the above details of the British Museum specimens of *G. bottai*) were thus (I. R. Bishop in litt., 20 April 1977; P. D. Jenkins in litt., 20 August 1977): "Apart from the difference in size, the young skull differs from your specimen in that the lateral pterygoid fossae are smaller and hemispherical in shape. The supraorbital ridges not so pronounced and the lip of the auditory meatus less prominent." These discrepancies can all be attributed to differences between juvenile and adult skulls.

Furthermore (Jenkins in litt., 25 August 1977) "both B.M. skins have white patches behind the ear but not so distinct as in your specimen. The dorsal coloration is similar although the flanks are not so bright. The ventral is pure white [as in the two recent specimens, author]. The tail of the young specimen is apparently entire and shorter in length than the head and body, unlike your specimen. The tail of our other specimen is broken (B.M. 46.6.2.44) but bears the following comment on its label: 'other specimen sent by Sundevall has tail 115 mm long.' " This 'other' specimen remains unknown. Differences between the recent specimen and the British Museum *bottai* might be attributed to age (changes of which are completely unknown). All subsequent conclusions and measurements, especially of the single juvenile, are necessarily based on that material.

Allen (1939) listed *bottai* as a species of the genus *Dipodillus* Lataste, 1881 which, in his use of this taxon of naked-footed gerbils, included short-tailed as well as long-tailed species of gerbils. Ellerman (1941) regarded *Dipodillus* (including *Hendecapleura*) as one of the two subgenera of *Gerbillus* Desmarest, 1804, but did not allocate *bottai* to either of the two taxa and did not list it under the forms seen, despite two specimens present in the British Museum.

The identification of specimens recorded for the Air region (Niger) as *G. bottai* by Dekeyser (1950)

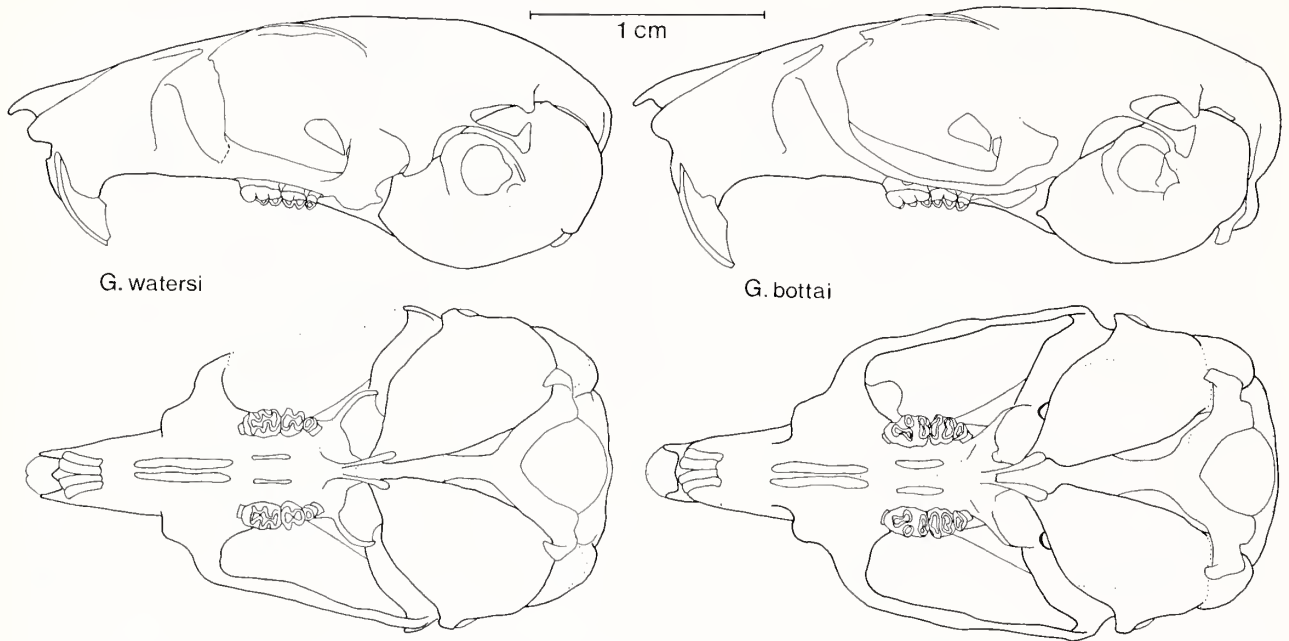


Fig. 1 (left).—Skull of *Gerbillus (Hendecapleura) watersi* (B.M. 1.5.5.56) lateral (upper) and ventral (lower) side. Fig. 2 (right).—Skull of *Gerbillus (Hendecapleura) bottai* (SMF 50159) lateral (upper) and ventral (lower) side (all drawings by Gieela Krebs).

seems highly doubtful and has not been confirmed (compare Petter 1975). The length of the upper molar row is shorter (3.0–3.2) than in *G. bottai* and the specimens were discussed as related to *G. principulus* Thomas and Hinton, 1923 (a subspecies of *G. nanus* with large bullae), and *G. stigmonyx luteolus* Thomas, 1901. Setzer (1956), within the subgenus *Dipodillus*, accorded a separate grouping to *bottai* because of small auditory bullae, open pterygoid fossae (but see note on juvenile B.M. skulls above), and more massive cheekteeth in proportion to the size of the skull, which is confirmed by the present material; *G. bottai* differing mainly in size from *G. stigmonyx* Heuglin, 1877, and *G. lowei* Thomas and Hinton, 1913. A third group, including *G. watersi* DeWinton, 1901, *G. mackillingini* Thomas, 1904, *G. principulus* Thomas and Hinton, 1923, and *G. muriculus* Thomas and Hinton, 1923, is similar to *G. bottai* in body size, but the group differs by more greatly inflated auditory bullae, relatively closed pterygoid fossae, and small cheekteeth. The last three taxa are currently considered to be subspecies of *nanus* and the differences noted by Setzer (1956) are confirmed by the material listed above.

Petter (1968, 1975) states that no external measurements of the only two existing *G. bottai* specimens are known, but in his key this species is dif-

ferentiated from others by a tail shorter than the head and body length. This confirms the conclusion that *G. bottai* is represented only by the specimens in the British Museum, the skins of which are without measurements (Setzer, 1956) and one of which has a broken tail. The two recent specimens from the Sennar region differ from *G. nanus* by considerably narrower braincase, narrower interorbital width, much smaller bullae, and thus with pterygoid fossae more open, a larger suprameatal triangle, and heavier cheekteeth. They differ from *G. garamantis* and also from *G. watersi* (Fig. 1) by larger skull, heavier cheekteeth, less inflated bullae, and more open pterygoid fossae; *G. watersi*, however, has a thin tuft on the tail (like *G. bottai*).

Both recent specimens differ from *G. pusillus*, of which only a juvenile skull is available to me, by slightly larger molars, second lamina of M^3 reduced to a single cusp, and lighter colored incisors. They differ from *G. henleyi jordani* by larger size in all skull measurements; relative to the size of skull the bullae are less inflated in their anterior part.

G. campestris venustus (Sundevall, 1843), as identified and recorded by Happold (1967b) from east of the Nile north of Khartoum and from north of the Blue Nile, is larger in all measurements and has long fur and a heavy tuft on the tail. The *G. cam-*

pestris specimens listed above differ in the same way and additionally have a more closed pterygoid fossae.

The description of *Meriones stigmonyx* Heuglin, 1877, regarded as a subspecies of *G. campestris* (see Petter, 1975), is insufficient for a specific determination, except for its long tail (head and body 71.4–78, tail 104–120, hind foot 19.3, ear 10.8–13.0; converted from “pied du roi” = French foot, 1 line = 2.174 mm). This insufficiency was noted by Thomas (1901) who additionally remarked that a specimen in the Stuttgart Museum, identified as *G. stigmonyx*, does not agree with Heuglin’s (1877) description.

Despite these facts, *G. luteolus* Thomas, 1901, was attached to *G. stigmonyx* as a subspecies. The skull measurements of *G. s. luteolus* show only a fair agreement with the two recent specimens, which might be due to different methods of taking measurements. *G. s. luteolus* bears close resemblance to the two specimens under discussion in the distribution of white on the head, including a darker nose patch, and with some tiny scattered hairs in the distal part of the hind feet. This is also the main character by which Thomas (1901) separated *G. s. luteolus* from the more northern (sic) *bottai*. This gerbil has been recorded from the area between the White Nile and Blue Nile (in other words the Gezira) as *G. stigmonyx* (including *luteolus* as a synonym) by Setzer (1956). The type locality of *G. stigmonyx* was given as “near Khartoum” but there is no convincing reason to restrict it to the south side of Khartoum.

As understood by Happold (1967b), *G. stigmonyx* has some resemblance with the specimens discussed here; it is smaller than *G. campestris venustus*, with shorter fur and less tufted tail.

An additional specimen of this group from Jebel-ein (AMNH 88219) agrees well with the characters given above (for measurements see Table 1)—naked and short hind feet, nearly unicolored and weakly tufted tail, postauricular spot not very prominent (like the B.M. specimen), hairs of underside pure white, nose spot not set off from color of head, M^3 with only one lamina (as approached by the left M^3 of SMF 50159), and bullae small.

Happold (1967a) does not give locality records for gerbils within the Khartoum Province, but his *G. campestris venustus* were collected north of the Blue Nile (Happold, 1967b), only *G. watersi* was recorded from south of Khartoum (Happold, 1969), and no gerbils were found in the Funj area. Thus,

G. stigmonyx, *bottai*, and *watersi* are the only naked-footed gerbils recorded from the region between the two Niles in the Sudan.

In the combination of characters as detailed above, there are no similar species of either *Dipodillus* or *Hendecapleura* known from Egypt (Flower, 1932; Setzer, 1958; Hoosgraal, 1963) or Libya (Ranck, 1968).

Of northeastern African *Hendecapleura*, larger size excludes *G. campestris somalicus* Thomas, 1910, inflated bullae characterize *G. nanus brockmani* Thomas (1910) and *G. watersi* (see Petter, 1975; Roche, 1976). Similarities are to those gerbils which have relatively uninflated bullae—*G. pusillus* and *G. harwoodi*.

From its description and published measurements (Thomas, 1901; Hollister, 1919; Roche, 1976), *G. harwoodi* seems to be very close to *G. bottai*, but my comparative material is insufficient (Table 1) to prove a synonymy of these; Roche (1976) emphasizes the darker coloration of *G. harwoodi* in contrast to *G. pusillus*, which is also true for *G. bottai*.

It cannot be excluded that some of the specimens listed by Yalden et al. (1976) as *G. ruberrimus* Rhoads, 1896 (which included *G. harwoodi* as a synonym), belong to *G. bottai*.

The above comparisons suggest regarding *G. stigmonyx* Heuglin, 1877, as a *nomen dubium* and uniting *G. luteolus* Thomas, 1901, and *G. harwoodi* Thomas, 1901, under the older name *G. bottai* Lataste, 1882, which would belong to the subgenus *Hendecapleura* as redefined by Schlitter and Setzer (1972).

Sennar (or in other spellings, Senar, Sennaar, Senaar) was an independent kingdom of the Funj, which was destroyed politically by the advance of Arabs into the Bilad As-Sudan (the country of the black). It stretched northward to Khartoum and comprised most of the Blue Nile Valley to the south, in what is now the Republic of the Sudan, and westward to the White Nile (that is, the Nile above Khartoum to Lake No) into the area of today’s Kosti. There was a boundary with the Nilotic Shilluk tribe; the Nilotic place names in that area disappeared only at the end of the last century. After the fall of the Sennar kingdom, the modern town of Sennar was the capital of the region, but also had an alternative name—Makwar; the first Blue Nile Dam at Sennar was named Makwar Dam after its construction in the second decade of this century.

Customs and traditions changed only slowly; do-

mestic pigs were kept and eaten a hundred years ago and were still offered for sale to Europeans in 1960. The name "Sennar" for a geographical region was gradually replaced by the Arabic designation "Gezira," meaning the island (between the two Niles). During the British rule, the Blue Nile Province was formed, and Sennar became a district.

To the early travellers and explorers, Sennar was but the region, and not a place or town. Bruce (1791) described the position of Sancha as on the border between Sennar and Ethiopia. Eduard Rüppell, who explored in the northern Sudan, sent his hunter to collect along the Blue Nile; all this material now in the Senckenberg Museum is labelled "Sennar." This is also valid for other collections and has sometimes been used in a very liberal way, as for *Gazella dama ruficollis* (H. Smith, 1827) from

Sennar, listed by Setzer (1956); there was never in recent times a *dama* gazelle to the east of the Nile.

Occasionally the meaning of Sennar remains completely obscure to its user; Elliot (1912) describes the distribution of *Papio cynocephalus* as Nubia, Central and East Africa in Sennar.

Many species were described from Sennar (compare list of synonyms in Setzer, 1956) and in most cases if not all, this has to be identified as *terra typica*, not as a *locus typicus*. If in the early descriptions of species from the Blue Nile region the habitat is given as Sennar, and other places which can be more precisely identified, like Sennar and Fazoglo (= Fazughli) for *Rhinopoma sennaariense* Fitzinger, 1866, preference should be given to the second habitat name as type locality (Kock, 1969), especially as there is no hill at Sennar where these bats could find a cave to shelter.

ACKNOWLEDGMENTS

I wish to thank Arnold H. Hoppe, Marrakech, for collecting these interesting specimens and I. R. Bishop and P. J. Jenkins of the British Museum (Natural History), London, for sending information, taking measurements, and making comparisons with the material under their care. The results of this paper were presented during the Colloquium on the taxonomy and ecology of African small mammals, sponsored by the Carnegie Museum of Natural History, Pittsburgh (19–22 September 1977) thanks to

a generous grant of the Senckenbergische Naturforschende Gesellschaft, Frankfurt a.M., and a financial support of the Deutsche Forschungsgemeinschaft, Bad Godesberg, which enabled me to study the collection of the American Museum of Natural History, New York. Dr. K. F. Koopman is to be thanked for making available unpublished material in the AMNH collection and for the friendly support I received from him.

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KARYOTYPE OF *GERBILLUS PYRAMIDUM* I. GEOFFROY (RODENTIA, GERBILLIDAE) FROM SENEGAL

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ABSTRACT

Gerbillus pyramidum is reported from Senegal for the first time. The external and cranial measurements and karyotype of

the female specimen are presented.

INTRODUCTION

A large hairy-footed gerbil was collected for the first time in Senegal near M'Boro (15°12'N, 16°55'W), in December 1975 by W. Böhme, during a scientific expedition (for details of this excursion see Böhme, 1978).

This specimen is a large female; its dorsal fur is

orange-fawn in color, but rather pale. The hairs of the middle of the back have a gray base; those of the sides are white. The belly is pure white. A dark line surrounds the eye; there is a white spot just behind the eye and another behind the ear. The vibrissae are pale or dark.

RESULTS

External measurements are given to the nearest millimeter. Cranial measurements were taken with a dial caliper and recorded to the nearest tenth of a millimeter. The bullae are measured as indicated by Ellerman and Morrison-Scott (1951), that is from the paraoccipital process to the anterior tip of the bulla. Length of feet includes the claws.

External and cranial measurements were as follows: head and body, 122; tail, 156; ear, 14; hind

foot, 34; occipitonasal length, 34.8; greatest zygomatic breadth, 19.1; least interorbital constriction, 6.1; length of maxillary toothrow, 4.8; auditory bulla, 9.3.

The karyotype was prepared by the "air-drying" method and shows 40 chromosomes—18 pairs of biarmed chromosomes and one pair of small acrocentrics (Fig. 1). The two X-chromosomes are metacentrics. The FN is 78 arms.

DISCUSSION

According to Petter (1975), the morphological characters and the measurements are those of *Gerbillus pyramidum* I. Geoffroy, 1825. The karyotype (2N = 40) is closely related to those published by Matthey (1952), from Beni Abbes, Algeria, by Wharman and Zahavi (1955) also from Algeria, by Jordan et al. (1974) from Tunisia, and by Lay et al. (1975) from Morocco. These last authors still distinguished *Gerbillus pyramidum tarabuli*, with 2N = 40, from *Gerbillus pyramidum pyramidum*, whose karyotype, with 38 chromosomes, is similar to that described by Wassif et al. (1969) from Egypt.

The Senegalese specimen was collected in a very dry coastal area consisting of wind-blown sand dunes of quaternary origin; herpetologically these sand dunes are characterized by lizards with northern (Palearctic) affinities (for example, *Acanthodactylus dumerili*, *Scincus albob fasciatus*, *Chalcides sphenopsiformis* and so on). The rather large measurements of the Senegalese specimen agree with those of the other specimens collected south of the Sahara (Rosevear, 1969; Setzer and Ranck, 1971). It presented the same morphological details as those described by Lay et al., 1975: "tympanic and

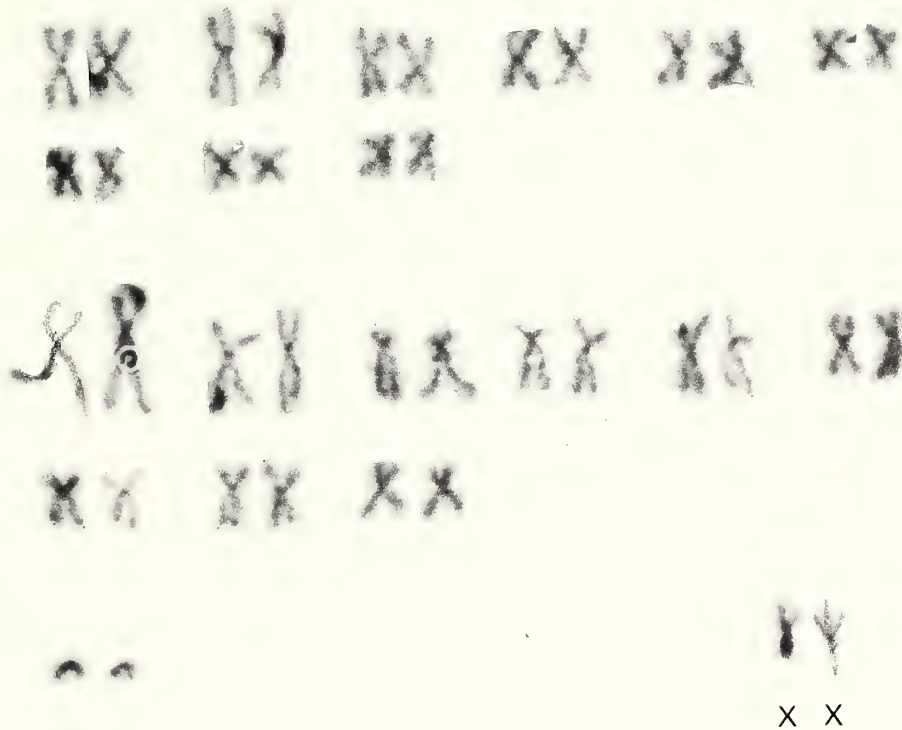


Fig. 1.—Karyotype of a female *Gerbillus pyramidum* from M'Boro, Senegal.

mastoid components of the auditory bullae are distinctly less voluminous in *G. pyramidum*, the anterior end of the basio-occipital contacts the medial walls of both tympanic bullae and is relatively narrower in the Algeria-Morocco sample; the posterior palatine foramina are shorter and more constricted; the nasal-frontal bone contact is broad in *G. pyramidum* and narrow in the Algeria-Morocco sample."

This gerbil, whose chromosomes are nearly all metacentrics, and whose karyotype, the first known

south of the Sahara, is homogenous with the other populations of *Gerbillus pyramidum* from Africa, seems to be particularly closely allied with the specimens from Morocco. A hypothesis is that these individuals have been derived from a single ancient population that existed throughout the Sahara; however the communication is now broken, as it is for *Mastomys* (Tranier, 1974). An extensive collection of *Gerbillus* from this area and other similar but distant areas would allow completion of this study.

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KARYOLOGICAL AND MORPHOLOGICAL COMPARISONS OF
LEMNISCOMYS STRIATUS (LINNAEUS, 1758) AND
LEMNISCOMYS BELLIERI VAN DER STRAETEN,
1975, FROM IVORY COAST
(MAMMALIA: MURIDAE)

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ABSTRACT

The differences between two species of the *Lemniscomys striatus*-complex of Ivory Coast are described with the help of karyological, morphological, and biostatistical techniques. *Lem-*

niscomys s. striatus has a chromosomal set of 44, whereas *L. bellieri* has $2N = 56$.

INTRODUCTION

Two forms of the *Lemniscomys striatus*-complex are known to occur in Ivory Coast. One we consider to be typical *Lemniscomys striatus*, the other is *Lemniscomys bellieri*.

The original description of *Lemniscomys striatus* by Linnaeus (1758) is so incomplete and vague that it can be matched to any of the known forms of the *striatus*-complex. Moreover the original type locality "India" mentioned by Linnaeus is clearly erroneous. Thomas (1911), in trying to solve this problem, concluded that the specimen described by Linnaeus probably came from Sierra Leone.

When we consider the geographic distribution of the *Lemniscomys striatus*-complex as it is actually known and that the original type-specimen undoubtedly came from a region not too far from the seashore, we have to conclude that the specimens of the forest-belt of the Ivory Coast are to be assigned to typical *Lemniscomys striatus*. This form

lives in the clearings of the forest, at the fringes of the forest, in the cultivated areas near the villages, and in the more or less forested savannah.

In this publication we will discuss the biometrical and karyological differences, which enabled us to describe *Lemniscomys bellieri* as a new species (Van der Straeten, 1975b). As far as is known this new species inhabits the Guinean savannah (arborated and gras savannah) as well as the doka savannah of Ivory Coast and Ghana. In a forthcoming paper, we will show that *Lemniscomys bellieri* is related to *L. macculus* of eastern Africa.

In eastern Africa (more specifically northern and eastern Zaïre, southern Sudan, Ethiopia, Uganda, Rwanda, and Burundi) there coexists, just as in Ivory Coast, a bigger (*L. s. striatus* or *L. s. massaicus*) with a smaller (*L. macculus*) form of the *Lemniscomys striatus*-complex.

MATERIAL AND METHODS

For this study we were able to examine the very important collections made in Ivory Coast by our friend and colleague Dr. L. Bellier during the period 1963–1971. These collections were kindly made available to us by the O.R.S.T.O.M.

Out of this very important collection we studied 251 specimens of *Lemniscomys bellieri*, all of which were captured in Lamto (06°12'N; 04°58'W). The 395 specimens of *Lemniscomys s. striatus*

we included in this study were obtained in Adiopodoumé (05°20'N; 04°08'W), Dabou (05°21'N; 04°26'W), Lamto, and Mopoyem (05°19'N; 04°30'W). All of this material will later be deposited in the Muséum National d'Histoire Naturelle (Paris-France) and in the Koninklijk Museum voor Midden-Afrika (Tervuren-Belgium). The complete list of the specimens is published in Van der Straeten (1975a).

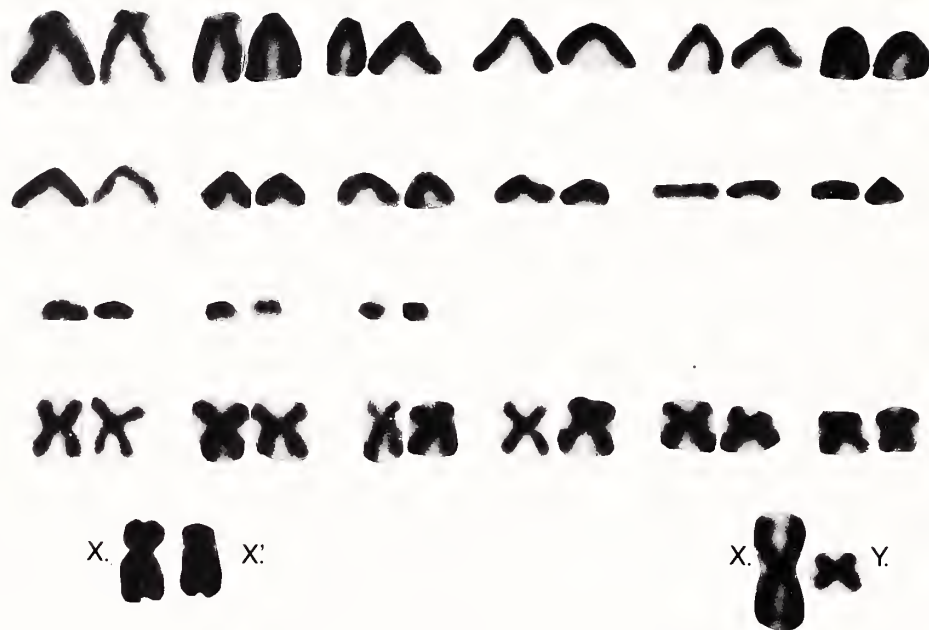


Fig. 1.—Karyotype of a male *Lemniscomys s. striatus* (coll. no. 846) and sex chromosomes of a female *L. s. striatus* (coll. no. 807).

The chromosome slides with the air-dried preparations were made in the Laboratoire d'Ecologie animale of the O.R.S.T.O.M. in Adiopodoumé, Ivory Coast, during February and March 1972. The eight specimens of *Lemniscomys bellieri* (six males and two females) were captured in Lamto and produced 74 (57 male and 17 female) countable mitoses spreads from which 12 (seven male and five female) were selected for measuring. All of the karyological results for *Lemniscomys striatus striatus* were obtained with five specimens (two males and three females) from Dabou and 10 (four males and six females) from Adiopodoumé. Together they produced 198 (62 males and 136 female) countable mitoses spreads, from which 55 (21 male and 34 female) were measurable. The following specimens in the Koninklijk Museum voor Midden-Afrika (collector numbers in parentheses) were those from which air-dried karyological preparations were made: *Lemniscomys bellieri*, Lamto (males—1275, 1276, 1282, 1331, 1334, 1339; females—1266, 1279); *Lemniscomys s. striatus*, Adiopo-

doumé (males—29, 569, 1010, 1104; females—119, 568, 1145, 1176, 1312, 1386); *L. s. striatus*, Dabou (males—830, 846; females—807, 831, 848).

Skull measurements and statistical methods are the same as used in former studies (Van der Straeten and Van der Straeten-Harrie, 1977; Van der Straeten and Verheyen, 1977). The 18 measurements which were used are enumerated in Table 3. The external measurements were copied from the labels. The hind foot length was measured with the nail.

The air-dried preparations were made following the slightly modified method of Hsu and Patton (1969). The chromosomal measurements were taken with a curvimeter; each measurement was taken 10 times, after which the mean was calculated. These data were used to pair the chromosomes. This pairing procedure was executed with an IBM 1130 computer and a FORTRAN program.

RESULTS

Description of Karyotypes

Lemniscomys striatus striatus.—Of the 198 counted mitoses spreads, 78.8% have $2N = 44$ and $NF = 72$. The karyotype is composed of eight pairs of telocentric chromosomes, seven pairs of subtelocentric chromosomes, six pairs of metacentric chromosomes, and 1 pair of sex chromosomes XX' or XY (see Figs. 1 and 2). The X-chromosome is the largest metacentric chromosome; the X' the only submetacentric one. The Y-chromosome could

not be identified with absolute certainty but we suppose that it is the smallest metacentric chromosome.

It is remarkable that in the females the sex chromosomes form a heterogenic pair. The difference between the X and X' chromosome is due to a difference in length of the short arms.

In some of the telocentric chromosomes a very short additional arm can be observed; it is possible that a number of them should be considered to be acrocentric. However the quality of the preparation

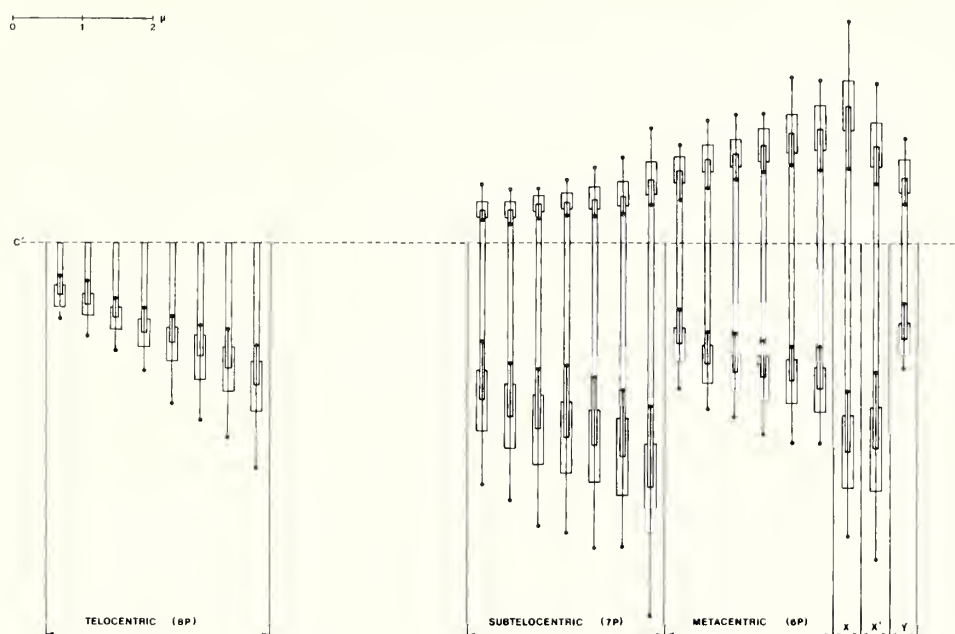


Fig. 2.—Graph showing karyotype of *Lemniscomys s. striatus*. Mean, mean \pm standard deviation, and range are indicated for each chromosome.

and the photographs did not allow further investigation.

With the exception of the sex chromosomes we could not find a difference between the male and female karyotype.

Lemniscomys bellieri.—Of the 74 studied mitoses spreads, 55.4% show a diploid number of 56 ($= 2N$) and a fundamental number of 78 ($= NF$). The karyotype is composed of 17 pairs of telocentric chromosomes, seven pairs subtelocentric chromosomes, three pairs metacentric chromosomes, and one pair of sex chromosomes XX' or XY (see Figs. 3 and 4).

In this species the X-chromosome is also the largest metacentric of the karyotype and the X' chromosome is submetacentric. The Y-chromosome is the

second longest metacentric or is perhaps submetacentric. Here also the sex chromosomes of the female form a heterogenic pair XX' .

There is a certain similarity between the karyotypes of *L. striatus striatus* and *L. bellieri* when we

Table 2.—Eigenvectors of 19 variables for the first three canonical variates.

Variable code	1	2	3
HL	0.5831	0.1932	-0.3783
GRLE	-0.9375	-0.4675	0.3525
PRCO	0.4559	3.8381	-0.2940
HEBA	0.3818	-2.6529	0.4863
HEPA	0.7462	-0.4103	0.9431
PAF	-0.0886	1.1638	0.5596
DIA1	-0.3928	-3.4485	-1.6678
DIA2	-0.6140	0.5533	-0.6217
INT	2.2791	-0.6067	1.6093
ZYG	0.2112	0.4286	0.9798
UPTE	0.0120	-1.9578	-0.2864
UPDE	-0.7466	1.6011	1.4716
M^1	4.3813	-1.5595	-13.0248
ZYPL	-0.1754	0.2801	-0.8379
BNAS	-0.5152	-1.2736	-2.1432
LNAS	1.0952	0.2441	-0.5363
LOTE	0.3778	0.7545	-0.1532
BUL	-4.1282	-0.0960	-1.4002
BRCA	0.4681	-0.8785	-0.0589

Table 1.—Eigenvalues of the canonical transformation with test of significance.

No.	Eigenvalue	Relative importance (%)	Chi-square	Degrees of freedom	Probability
1	373.792	81.7	872.046	76	1.000
2	61.164	13.4	269.359	54	1.000
3	14.264	3.1	83.239	34	0.999
4	8.260	1.8	31.069	16	0.987



Fig. 3.—Karyotype of a male *Lemniscomys bellieri* (coll. no. 1275) and sex chromosomes of a female *L. bellieri* (coll. no. 1279).

consider the X-chromosome, the X'-chromosome, and the seven pair of subtelocentric chromosomes.

Canonical Analysis

For the canonical analysis, we used 397 specimens collected in four localities and divided as follows in five groups: 1, *Lemniscomys s. striatus*, Adiopodoumé (25 specimens); 2, *Lemniscomys s. striatus*, Dabou (74); 3, *Lemniscomys s. striatus*, Mopoyem (88); 4, *Lemniscomys s. striatus*, Lamto (43); 5, *Lemniscomys bellieri*, Lamto (167).

We based this analysis on 18 skull measurements (see Table 2) and one external measurement (the hind foot length). The four canonical variates differ significantly from O. The first contains 81.7% of the total variation; the first and second together represent 95.1% of the total variation. In Table 1 we give the eigenvalues of the canonical transformation and in Table 2 the eigenvectors of the 19 variables for the first three canonical variates. Starting from these eigenvectors a graphical representation is made. For each group the center and the most extreme values are indicated by a polygonal delimitation. In Fig. 5 we give the graphical representation of the first and second canonical variate.

The first canonical variate shows a very clear division between two groups—*Lemniscomys bellieri* and *L. s. striatus*. The overlap is very small. The second canonical variate separates *Lemniscomys s.*

striatus in two subgroups depending upon their geographic origin; one subgroup includes the specimens from Adiopodoumé-Dabou and the other includes animals from Lamto-Mopoyem. The overlap, however, is extensive. The third canonical variate gives no further information.

When we consider the same species but now with the specimens grouped in age-classes we obtain similar results. Indeed, the first canonical variate separates *L. bellieri* from *L. s. striatus*, whereas the second variate separates the specimens on the basis of age.

Finally, if we consider the same species but now grouped following age and collecting locality similar results are obtained. The first variate separates *bellieri* from *striatus* and the second one separates the specimens according to age. In the second variate the differences between the subgroups Adiopodoumé-Dabou and Lamto-Mopoyem remain when one compares animals of comparable age groups.

Taxonomical Characters and Discrimination Analysis

Lemniscomys bellieri is in its overall measurements clearly smaller than *L. s. striatus* (Table 3). This is especially true for the hind foot length of the adults—*L. bellieri* 25.4 mm (23.0–27.0); *L. s. striatus* 26.0 mm (24.0–31.0).

Both species differ also strikingly in their dorsal

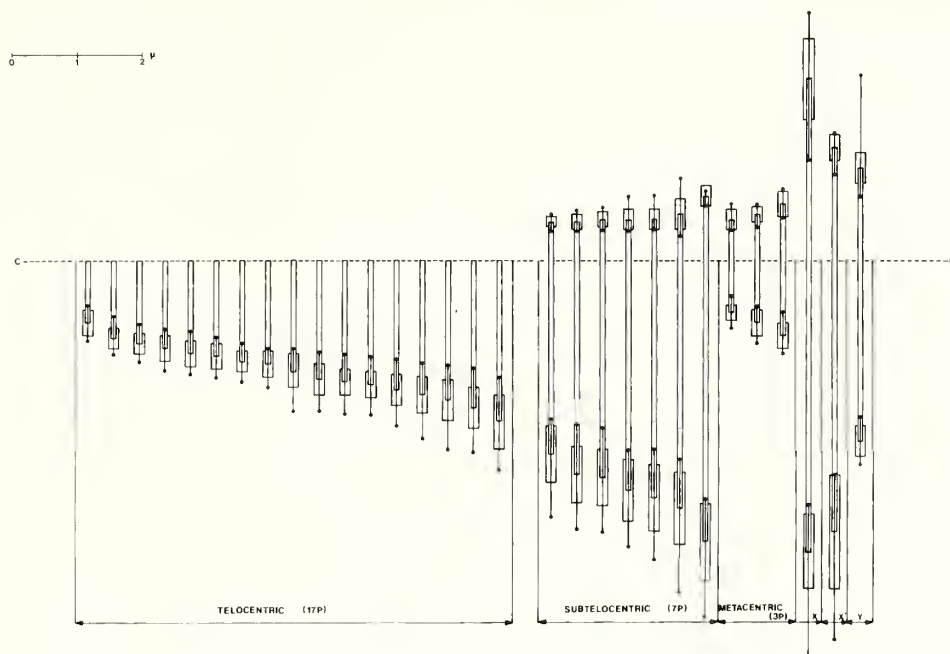


Fig. 4.—Graph showing karyotype of *Lemniscomys bellieri*. Mean, mean \pm standard deviation, and range are indicated for each chromosome.

pelage pattern. *L. s. striatus* has on both sides of its black mediodorsal stripe, eight light longitudinal stripes, each of which on closer examination is composed of a row of individualized spots (more to the eastern part of Africa-Zaire and Ethiopia—we find specimens of *L. s. striatus* where the individual spots show the tendency to blend into a set of continuous longitudinal light stripes). *Lemniscomys bellieri* also shows eight light longitudinal stripes on each flank and a sharply defined black mediodorsal line. It must be noted, however, that only the third, fourth, and fifth stripes are clearly outlined. The individual spots are not neatly defined and melt more or less away in the darker background, resulting in an even more fuzzy dorsal pattern.

Lemniscomys s. striatus is craniometrically larger than *L. bellieri* and M_1 of *L. s. striatus* has mostly an Sm, which is generally absent in *bellieri*.

Notwithstanding all these morphological and metrical characters, a correct determination can give some difficulties when one examines only a skull. For this reason, we calculated two discriminant functions. Because these functions are based

on museum material exclusively from Ivory Coast, it is obvious that the proposed functions can only be used on Ivory Coast specimens.

For the first discriminant function we used all of the 18 cranial measurements as well as the hind foot length (including nail). The data for 229 specimens of *L. s. striatus* were included as well as the data for 167 specimens of *L. bellieri*. The first discriminant function is calculated as follows: $K = 2.416 \times HL + 7.517 \times INT + 16.284 \times M^1 + 2.553 \times LNAS - 16.525 \times BUL - 70.229$. If $K > 0$, then we are dealing with *L. s. striatus*, if $K < 0$, then it is *L. bellieri*. The chance of misidentification is 3.5%.

The second discriminant function concerns only the cranial measurements and was computed with the same data as the first. It is calculated as follows: $K = 4.320 \times HEPA - 3.985 \times DIA\ 2 + 8.427 \times INT + 2.772 \times LNAS - 13.470 \times BUL - 23.793$. If $K > 0$ then the specimen is a *L. s. striatus*; if $K < 0$, it is a *L. bellieri*. The chance of misidentification here is 6.2%.

DISCUSSION AND CONCLUSIONS

There can be no doubt that two species of the *Lemniscomys striatus*-complex exist in the Ivory

Coast—the smaller *L. bellieri* and the larger *L. striatus striatus*. It was possible to describe *L. bel-*

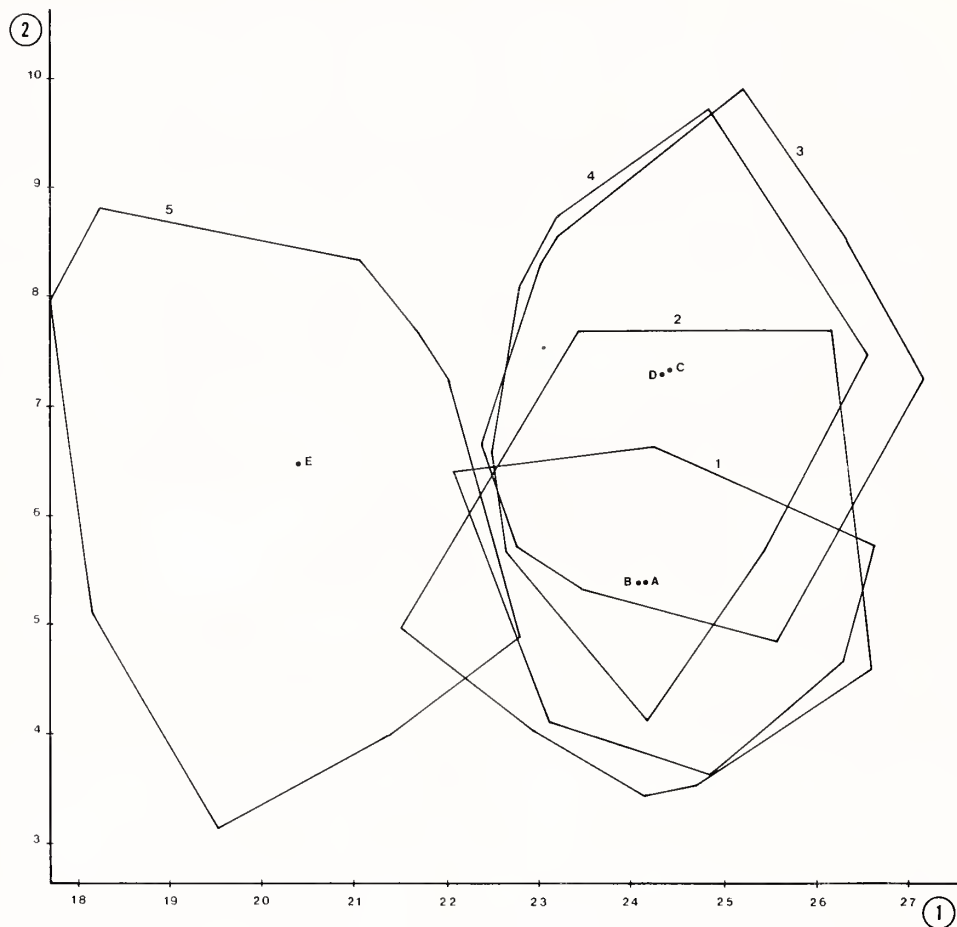


Fig. 5.—Canonical analysis: canonical means (solid circles) and extreme limit of each cloud of points; canonical variates I (abscissa) and II (ordinate); 1 (A) *Lemniscomys s. striatus* from Adiopodoumé, 2 (B) *L. s. striatus* from Dabou, 3 (C) *L. s. striatus* from Mopoyem, 4 (D) *L. s. striatus* from Lamto and 5 (E) *L. bellieri* from Lamto.

lieri as a new species because we are in the possession of a very important series of skins and skulls, which allowed a biostatistical approach, and we made air-dried preparations for karyological study.

In all of the older museum collections we were able to examine, we found only two specimens of *L. bellieri* (British Museum Natural History, 23.2.3.42 and 23.2.3.43, collected in 1922 by Lowe and Hardy in Béoumi, Ivory Coast). Both animals were labeled as belonging to the species *L. striatus*. Rosevear (1969), who studied these specimens, noted that they are smaller and show an aberrant dorsal pattern. He explained both characteristics by stating that the specimens are juveniles, which is clearly an error because the teeth and the skull sutures show that we are dealing with adults.

The dorsal stripe pattern of *L. bellieri* shows a certain similarity with that of *L. striatus venustus*. However, in all other respects both are very different. Indeed, the latter is the largest form of the *Lemniscomys striatus*-complex, whereas *bellieri* is the smallest.

The karyotypes of *L. s. striatus* and *L. bellieri* show certain similarities in the X and X' chromosome as well as in the seven pairs of subtelocentric chromosomes. Matthey (1959) first described the chromosomes of *L. striatus*. The results of his study were $2N = 48$, four metacentric chromosomes, and NF difficult to establish but probably around 60. It is probable that this specimen belongs to an East African form of *L. striatus*. Regrettably, skin and skull were not prepared so that an exact determination of his specimen will remain impossible.

Table 3.—Measurements in mm of adult *Lemniscomys*. Number of specimens, mean, and range are given from left to right for each species.

Variable code	Description	<i>L. s. striatus</i>	<i>L. bellieri</i>
HB	Head and body length	331; 118.1 (61.0–170.0)	220; 109.8 (91.0–127.0)
TL	Length of tail	300; 114.1 (30.0–143.0)	186; 113.3 (70.0–134.0)
HL	Length of hind foot + nail	340; 26.0 (24.0–31.0)	211; 25.4 (23.0–27.0)
EL	Length of ear	317; 15.2 (10.0–18.0)	203; 15.9 (13.0–19.0)
GRLE	Greatest length of skull	317; 29.63 (23.30–33.35)	223; 28.25 (24.35–31.30)
PRCO	Prosthion—condylion	346; 26.66 (23.10–30.10)	240; 25.31 (22.35–27.75)
HEBA	Henselion—basion	346; 22.83 (19.10–25.70)	230; 21.47 (18.75–23.70)
HEPA	Henselion—palation	349; 12.27 (10.40–13.70)	244; 11.50 (10.20–12.85)
PAF	Length of palatal foramina	349; 5.83 (4.85–6.85)	240; 5.53 (4.80–6.30)
DIA1	Length of diastema	349; 7.17 (5.75–8.50)	242; 6.72 (5.80–7.75)
DIA2	Distance between the anterior border of the alveole of M ¹ and the edge of upper incisor	331; 7.70 (6.20–9.20)	225; 7.21 (6.15–8.20)
INT	Interorbital breadth	349; 4.87 (4.30–5.55)	241; 4.42 (3.85–5.05)
ZYG	Zygomatic breadth on the zygomatic process of the squamosum	328; 13.54 (11.95–15.30)	229; 12.82 (11.20–14.40)
UPTE	Length of upper cheekteeth	353; 5.35 (4.60–5.90)	250; 5.11 (4.60–5.65)
UPDE	Breadth of upper dental arch	330; 6.06 (5.20–6.95)	233; 5.82 (5.15–6.50)
M ¹	Breadth of M ¹	355; 1.66 (1.40–1.85)	248; 1.61 (1.45–1.75)
ZYPL	Breadth of zygomatic plate	350; 3.56 (2.95–4.20)	242; 3.35 (2.65–4.10)
BNAS	Greatest breadth of nasals	329; 3.34 (2.70–4.30)	230; 3.16 (2.70–3.65)
LNAS	Greatest length of nasals	317; 11.59 (9.30–13.60)	223; 10.64 (8.55–12.20)
LOTE	Length of lower cheekteeth	350; 5.09 (4.50–5.55)	251; 4.88 (4.45–5.45)
BUL	Length of auditory bulla	339; 4.94 (4.25–5.60)	239; 5.08 (4.55–5.70)
BRCA	Braincase breadth	345; 12.15 (11.05–13.00)	240; 11.69 (10.50–12.90)

ACKNOWLEDGMENTS

We wish to thank Dr. L. Bellier for the hospitality and help he provided us during our stay in Adiopodoumé (1972). Moreover this study had been made possible thanks to the important collections he made in Ivory Coast and which were kindly put at our disposal for further study by the Authorities of the O.R.S.T.O.M.

Our gratitude goes also to our colleagues Dr. G. Corbet and Mr. I. Bishop, who allowed us to examine the murid collections

of the British Museum of Natural History, to Mr. M. Michiels, who made the air-dried preparations and worked out the karyotypes, to Dr. F. Hebrant and Dr. Ir. J. Desitter, who assisted us with the computer programs and to Mrs. B. De Vry-Vanlinden for technical assistance.

A large part of this research was made possible by the research grant F.K.F.O. no. 955.

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REVISION OF THE GENUS *SACCOSTOMUS* (RODENTIA, CRICETOMYINAE), WITH NEW MORPHOLOGICAL AND CHROMOSOMAL DATA FROM SPECIMENS FROM THE LOWER OMO VALLEY, ETHIOPIA

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ABSTRACT

Based upon new records of *Saccostomus* from southwestern Ethiopia, a revision of the genus is considered. Morphometric and karyological evidence indicate two species should be rec-

ognized—*S. campestris* from southern Africa and *S. mearnsi* from eastern Africa.

INTRODUCTION

Seven rodents of the genus *Saccostomus* were collected during the summer of 1973 in the Lower Omo Valley, Ethiopia, during a paleontological expedition directed by Y. Coppens. These individuals are noteworthy because of their shaggy fur, uniformly brownish-gray in color, and consisting of

long, soft, and silky hairs. The belly of these specimens is paler than the back, but still definitely grayish, unlike the forms from southern Africa with their pure white belly and their sleek but less shaggy fur.

RESULTS AND DISCUSSION

Table 1 presents the main external and cranial measurements for the specimens collected in the Lower Omo Valley, Ethiopia; three specimens from the British Museum, one from Ethiopia (reported by Yalden et al., 1976) and two from Uganda; three specimens from the Museum National d'Histoire Naturelle (MNHN) de Paris with southern African origin, one of which is the specimen studied by Matthey (1958). The measurements published by Roche (1976) for a specimen from Somalia are also reported here. External measurements are given to the nearest millimeter; cranial measurements were taken with a dial caliper and reported to the nearest tenth of a millimeter.

The specimens from northeast Africa (Uganda, Ethiopia, and Somalia) have a gray belly, a long ear (more than 20 mm), a long tail (more than 50 mm), and a long maxillary toothrow (more than 5.0 mm). The three southern specimens from the MNHN have a white belly, a short ear (less than 20 mm), a short tail (40 mm), and a short maxillary toothrow (less than 5.0 mm). The same characters are present on all the specimens from southern Africa that I studied in the British Museum, particularly the cotypes of *Saccostomus campestris* Peters.

The karyotypes were observed for two individuals in 1973 by the "squash" method as described

by Matthey (1958), and for two others in 1976–1977 by the "air-drying" method. The slides are not very easily interpreted, but the chromosome number was always between 40 and 42, never exceeding this last number, in more than 20 metaphases observed (Fig. 1). Ford and Hamerton (1956) published a karyotype of $2N = 44$ for an individual of unknown origin, but Matthey (1958) considers that it is difficult material to interpret and that the number of chromosomes for *Saccostomus campestris* is $2N = 46$, as he personally observed on a specimen collected in the Cape Province, South Africa.

Ellerman (1941) thought that there was only one species of *Saccostomus*—*S. campestris* Peters. Misonne (1968) agreed with him, but Roche (1976) thought that his specimen from Somalia was closely related to the other specimens from the "north," and different from the southern African *Saccostomus campestris*. I think that Ethiopian specimens, which are different by their morphological characters, by their measurements, and by their karyotype, represent a distinct species together with all the *Saccostomus* from the north of this area in Africa (Ethiopia, Uganda, Somalia, and Kenya). Prior to the revision of Ellerman (1941), different species had been described from these countries as follows: *Saccostomus umbriventer*, Miller, 1910; *Saccosto-*

Table 1.—Selected external and cranial measurements of *Saccostomus* examined from the Museum National d'Histoire Naturelle, Paris, and the British Museum (Natural History), London.

Number	Sex	Origin	Head and body	Tail	Hind foot	Ear	Oc-cipito-nasal length	Zygo-matic breadth	Inter-orbital con-strict-ion	Upper molar row	Bulla	Obser-vations
1974—54	♂	Omo, Ethiopia	140	50	24	20	32.0	17.2	4.6	5.6	6.2	Gray belly
1974—55	♀	Omo, Ethiopia	144	56	22	23	35.1	19.1	4.4	5.6	7.3	Gray belly
1974—56	♀	Omo, Ethiopia	149	70	25	25	34.0	18.8	4.5	5.9	7.0	Gray belly
814	♂	Omo, Ethiopia	150	81	23	22	36.7	19.6	4.9	5.9	6.9	Gray belly
1977—1	♀	Omo, Ethiopia	137	58	22	20	36.2	19.5	4.5	7.0	7.0	Gray belly
1977—2	♀	Omo, Ethiopia	141	58	23	23	34.9	19.4	4.5	6.3	6.9	Gray belly
1977—3	♀	Omo, Ethiopia	153	67	24	24	36.2	19.5	4.4	6.2	6.2	Gray belly
BM 46.740	♀	Karamoja, Uganda	140	50	22	20	32.2	17.0	4.4	5.9	6.5	Gray belly
BM 71.450	♂	Karamoja, Uganda	—	—	—	—	34.5	18.0	4.7	5.8	5.9	Gray belly
BM 71.451	♂	Karamoja, Uganda	117	69	19.4	20.2	31.2	17.4	4.3	5.6	7.2	Gray belly
BM 73.490	♀	Maji, Ethiopia	116	64	22	21	—	—	—	—	—	Gray belly
3047—MF	♀	Giohar, Somalia	144	72	23	20	35.3	17.3	4.1	6.2	—	Gray belly
1958—226	♂	Transvaal, R.S.A.	125	40	22	17	35.7	17.8	4.7	4.5	8.0	White belly
1964—56	♂	Rhodesia	118	40	19	16	30.8	—	4.3	4.6	6.0	White belly
1969—57	♀	Rhodesia	122	40	19	17	32.4	—	4.5	4.3	6.4	White belly

Table 2.—Means, standard errors, and standard deviation of the lengths of the tail, the ear, and the upper molar row from different populations from the American museum collections. The measurements of the upper molar row were made by the author and permit statistical tests on the homogeneity of the different populations. The two groups are homogeneous and each different from the other. The specimens from Tanzania are different from the two groups, but their characters are reported to the second.

Origin	Num- ber of speci- mens	Length of the tail		Length of the ear		Length of the upper molar row		Significance
		Mean \pm standard error	Standard deviation	Mean \pm standard error	Standard deviation	Mean \pm standard error	Standard deviation	
Northern Rhodesia (AMNH)	63	47.5 \pm 0.7	5.39	18.2 \pm 0.1	0.76	4.68 \pm 0.03	0.27	F = 0.92 < 1
Angola (AMNH)	5	46.4 \pm 2.5	5.68	16.0 \pm 1.0	1.40	4.44 \pm 0.07	0.16	
Bechuanaland (AMNH)	17	42.8 \pm 0.8	3.51	17.2 \pm 0.4	1.63	4.57 \pm 0.06	0.23	
Nyasaland (AMNH)	23	39.3 \pm 1.1	5.13	16.4 \pm 0.2	0.86	4.57 \pm 0.03	0.14	homogeneous population
Southern Rhodesia (AMNH)	13	45.3 \pm 2.3	8.0	16.0 \pm 0.6	1.87	4.61 \pm 0.04	0.15	
South West Africa (AMNH)	5	48.1 \pm 3.1	6.97	18.5 \pm 0.8	1.70	4.69 \pm 0.28	0.63	
Transvaal (USNM)	13	46.2 \pm 2.2	8.12	17.7 \pm 0.4	1.42	4.68 \pm 0.07	0.25	
Bechuanaland (USNM)	14	44.1 \pm 1.1	5.13	16.9 \pm 0.3	1.21	4.71 \pm 0.05	0.21	
Mozambique (Gaza) (USNM)	13	44.0 \pm 1.4	4.59	17.3 \pm 0.3	0.90	4.49 \pm 0.05	0.18	t = 16.66 t > 1.96 significant difference
Mozambique (Tete) (USNM)	14	43.1 \pm 0.9	3.16	16.9 \pm 0.2	0.90	4.48 \pm 0.05	0.20	
Nyasaland (MCZ)	5	34.5 \pm 1.9	3.87	17.7 \pm 0.4	0.95	4.17 \pm 0.08	0.18	
Uganda (AMNH)	3	77.7 \pm 10.7	18.40	—	—	6.08 \pm 0.07	0.14	F = 0.67 < 1 homogeneous population
Kenya (USNM)	25	61.4 \pm 1.13	5.54	19.4 \pm 0.3	1.70	5.94 \pm 0.05	0.27	
Kenya (MCZ)	4	56.7 \pm 4.8	9.71	22.0 \pm 0.0	0.00	5.86 \pm 0.06	0.11	
Omo (MNHN)	7	62.9 \pm 3.9	10.46	22.4 \pm 0.7	1.90	6.07 \pm 0.18	0.49	
Tanganyika (AMNH)	29	48.8 \pm 1.2	7.2	—	—	5.38 \pm 0.04	0.21	significant difference



Fig. 1.—Karyotype of *Saccostomus mearnsi* from Omo Valley, Ethiopia.

mus mearnsi, Heller, 1910; *Saccostomus isiolae*, Heller, 1912; *Saccostomus cricetulus*, Allen and Lawrence, 1936. The holotypes of these species are deposited in the Smithsonian Institution, Washington, D.C., and at the Museum of Comparative Zoology, Harvard University.

The four species are closely related. The first described is *S. mearnsi*, the holotype of which is an adult male in good condition (better condition than *S. isiolae*, but younger than *S. unbriventer*, which is a very old female). *S. cricetulus* is not very different and when described by G. M. Allen and B. Lawrence they thought that the four species might be the same (Allen and Lawrence, 1936). I think that *Saccostomus mearnsi* is the available name for the northeastern species of *Saccostomus* characterized by a gray belly, a long tail (more than 49.0 mm), a large ear (more than 19.0 mm), a long maxillary toothrow (more than 5.0 mm), and a karyotype of $2N = 40-42$ chromosomes.

Table 2 shows the means of the length of the tail, the ear, and the upper molar row for a group of

specimens from the American Museum of Natural History, New York, from the United States National Museum, Washington, D. C., and from the Museum of Comparative Zoology, Harvard, collected in different countries of eastern and southern Africa. It shows the difference between the specimens from Zambia (Northern Rhodesia), Angola, Botswana (Bechuanaland), Malawi (Nyasaland), Zimbabwe (Southern Rhodesia), Transvaal, and Mozambique on one hand and from Tanzania, Uganda, Kenya, and Ethiopia on the other hand. The specimens from Kijungu, Tanzania, are referred to *S. mearnsi*, but they are a bit smaller than the individuals from the other northeastern countries, and statistically significantly different. Their karyotype is unknown.

An hypothesis to test is whether the division between the two species is the Rift Valley. Furthermore, it would be very interesting to collect some specimens in southern Tanzania or in northern Mozambique to test the possibility of speciation according to the latitude in this region.

SUMMARY

Two different species of *Saccostomus* are recognized—*S. campestris* from southern Africa, char-

acterized by a white belly, a short ear (less than 19 mm), a small tail (less than 49 mm), a short upper

molar row (less than 5.0 mm) and a karyotype of $2N = 46$ chromosomes; *S. mearnsi* from eastern Africa, characterized by a gray belly, a large ear,

a long tail, a long upper molar row and a karyotype of $2N = 40-42$ chromosomes.

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TAXONOMIC REVIEW OF THE FAT MICE (GENUS *STEATOMYS*) OF WEST AFRICA (MAMMALIA: RODENTIA)

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ABSTRACT

Data from specimens of West African taxa of *Steatomys* were subjected to univariate and multivariate statistical analyses. Geographic and nongeographic variation were analyzed based upon an examination of 385 conventional museum specimens. From the results of the analyses, three species of *Steatomys* are recognized in West Africa. *Steatomys cuppedius*, a small monotypic species, occurs in the Sahel and Sudan Savanna zones of

West Africa. *S. caurinus* exhibits geographic variation; two subspecies are recognized, one of which is described as new. *S. jacksoni* is retained as a unique species known only by the holotype from Ghana. Both *S. caurinus* and *S. cuppedius* exhibit a high degree of variation with age. Geographic distributions of the West African taxa are plotted based upon specimens examined and literature records.

INTRODUCTION

Fat mice of the genus *Steatomys* are members of the rodent family Muridae and together with the genera *Dendromys*, *Prionomys*, *Dendroprionomys*, *Leimacomys*, *Deomys*, and *Malacothrix* are included in the subfamily Dendromurinae. The phylogenetic affinities of the genera of this subfamily are little understood and the taxonomic relationships of the many described taxa are poorly known. Geographically, genera of this subfamily are distributed throughout subsaharan Africa in habitats ranging from subdesert to forest.

Species of the genus *Steatomys* occur throughout subsaharan Africa in habitats ranging from subdesert to degraded forest or forest edge. Generally, however, they are found in savannah. In spite of their widespread occurrence, specimens of the genus are not often taken because they do not readily enter any type of traps. In areas where individuals can be captured by hand at night or dug from their burrows, significant samples are being accumulated.

Initially, specimens were few and wide hiatuses existed between samples. During the last half of the nineteenth and early part of the twentieth centuries, individuals from each locality were usually described as a new taxon. There have been two major listings of the taxa in the genus. Allen (1939) listed 18 species with 26 subspecies, whereas Ellerman

(1941) gave 18 species with 24 subspecies, some of which differed from Allen's list.

Three species of *Steatomys* have been described from West Africa—*S. caurinus* Thomas, 1912, from Panyam, Nigeria; *S. cuppedius* Thomas and Hinton, 1920, from Farniso [=Panisau], Nigeria; *S. jacksoni* Hayman, 1936, from Wenchi, Ghana. Allen (1939), Ellerman (1941), and Rosevear (1969) considered these three taxa to be distinct species, based generally on the original descriptions. In a recent provisional checklist of the genus, Coetzee (1977) listed both *S. caurinus* and *S. jacksoni* as subspecies of *S. pratensis* Peters, 1846, and *S. cuppedius* as a subspecies of *S. parvus* Rhoads, 1896. Both *S. pratensis* and *S. parvus* were considered by Coetzee (1977) to be widespread savannah-occurring Panafrikan species. However, he has admitted to perhaps oversynonymizing the nominal taxa in his provisional checklist, wherein he recognized three species in the genus.

Relationships of the three West African forms to other species within the genus in the remainder of Africa is beyond the scope of the present study. A short review of described forms, which might occur sympatrically or parapatrically with these three taxa follows. *Steatomys opinus* Pousargues, 1894, originally described from material from the region now included in the Central African Empire, is

found in degraded forest and woodland savannah in central Africa (Coetzee, 1977). Because it is known to occur in the Cameroons, it might therefore also occur in the southern parts of West Africa, at least in southern Nigeria. A large species (greatest length of skull above 30), *Steatomys opinus*, is considered by Coetzee (1977) to be only subspecifically distinct from *S. pratensis*, a more geographically widespread species described originally from southern Africa. Three additional species occur in the Sudan (Setzer, 1956)—*S. aquilo*, *S. gazellae*, and *S. thomasi*. Coetzee (1977) also synonymized *S. aquilo*

and *S. gazellae* with *S. parvus*, and *S. thomasi* with *S. pratensis*.

The purpose of this study was to examine the systematic relationships of the nominal taxa of the genus *Steatomys* in West Africa, based on sizeable unreported collections in the Smithsonian Institution, Washington, D.C. Here West Africa is considered to be that portion of Africa west of the Nigerian border and south of the Sahara. This geographic limitation is not the same as that used by Rosevear (1965, 1969) who included those parts of Cameroon west of the Sanaga River.

MATERIALS AND METHODS

Conventional museum skins and skulls of 385 specimens of the genus *Steatomys* from West Africa were examined. All of the holotypes of western African taxa were examined by both authors. Five external and 14 cranial measurements were recorded, in millimeters, from nearly all specimens examined. External measurements were listed from the specimen labels; cranial measurements were taken with dial calipers. Definitions of these cranial measurements are given below:

Greatest length of skull.—Greatest distance from the anterior edge of the nasal bones to the posteriormost edge of the occipital bone.

Condylobasal length.—Greatest distance from the anteriormost projection of the premaxilla between the incisors to the posterior edge of the occipital condyles.

Zygomatic breadth.—Greatest distance across zygomatic arches at right angles to longitudinal axis of cranium.

Interorbital breadth.—Least distance across interorbital constriction.

Rostral breadth.—Least distance across the rostrum immediately anterior to the zygomatic plate.

Oblique length of bulla.—Greatest oblique length of auditory bulla, taken from a point adjacent to the paraoccipital process to the anteriormost edge of bulla.

Greatest length of bulla.—Greatest oblique length of bulla taken from the posterior edge of mastoidal bulla to the anteriormost edge of auditory bulla.

Length of maxillary tooththrow.—Least distance from the anterior edge of alveolus of M^1 to posterior edge of the alveolus of M^3 .

Breadth across upper molars.—Least distance, measured at right angles to the longitudinal axis of the skull, from the widest point on the labial edge of the crowns of M^1 in each maxillary tooththrow.

Length of anterior palatal foramen.—Greatest distance from anterior edge to the posterior edge of the anterior palatal foramen.

Length of posterior palatal foramen.—Greatest distance from the anterior edge to the posterior edge of the posterior palatal foramen.

Length of diastema.—Greatest distance from the posterior edge of the alveolus of the incisors to the anterior edge of the alveolus of M^1 .

Height of skull.—Greatest height of skull (taken perpendicular to the horizontal plane of skull when placed on a microscope slide).

Length of mandibular tooththrow.—Least distance from the anterior edge of the alveolus of M_1 to posterior edge of the alveolus of M_3 .

Univariate statistical analyses were performed on an IBM 360 computer at Carnegie-Mellon University, Pittsburgh, and multivariate statistical analysis on an IBM 370 computer at Texas Tech University, Lubbock. Univariate analyses of secondary sexual, age, and individual variation were performed using the UNIVAR program developed and published by Power (1970). Standard statistics (mean, range, standard deviation, standard error, variance, and coefficient of variation, among others) are generated by this program. In the event of two or more groups being compared, a single-classification analysis of variance (ANOVA) to test for significant differences between or among means is employed. When means were found to be significantly different, the Sums of Squares Simultaneous Test Procedure (SS-STP) was used to determine maximally nonsignificant subsets.

Multivariate statistical analyses were performed using the Numerical Taxonomy Systems (NT-SYS) package developed by F. J. Rohlf, R. Bartcher, and J. Kishpaugh at the University of Kansas. In these analyses the OTUs were grouped localities (geographical samples) and the values used for each measurement were arithmetic means for the measurement. Matrices of Pearson's product-moment correlation and taxonomic distance coefficients were computed. Cluster analyses were performed using the unweighted pair-group method using arithmetic averages (UPGMA) on correlation and distance matrices, and phenograms were generated for both. Only the distance phenogram is given as it gave larger coefficients of cophenetic correlation and the results of the distance phenogram also agree more closely with other analyses. Three principal components were extracted from the matrix of correlations, and a three-dimensional projection of the samples onto the three principal components was made. For the theory and use of these tests, see Sokal and Sneath (1963), Schnell (1970), Atchley (1970), Genoways (1973), and Sneath and Sokal (1973).

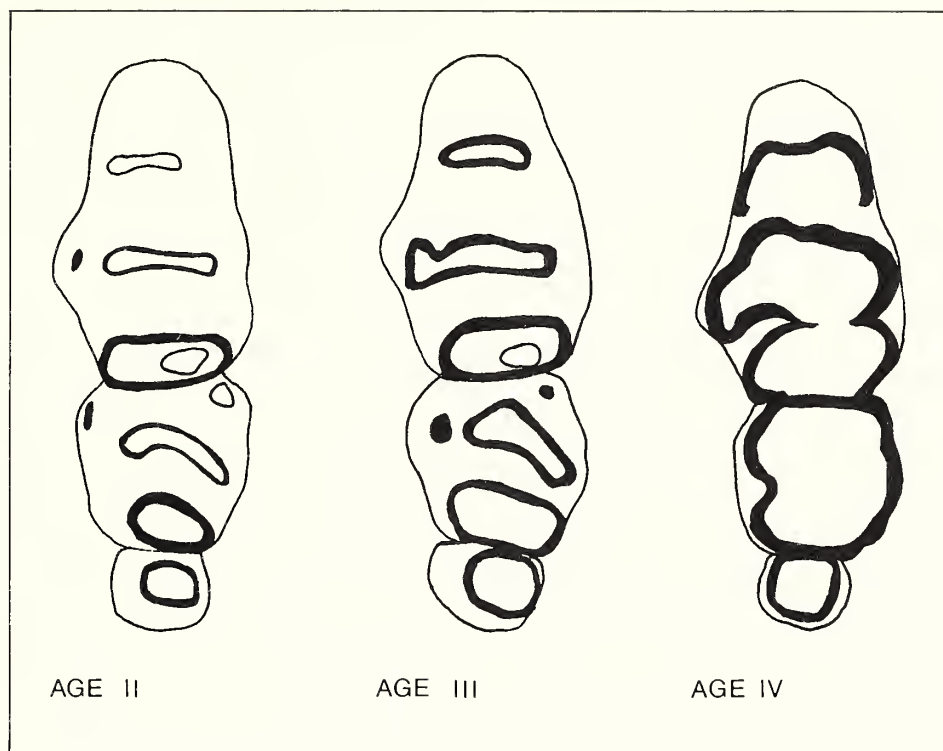


Fig. 1.—Diagrammatic representations (drawn from camera lucida) of left maxillary toothrows of *Steatomys cuppedius* illustrating wear pattern for age categories II, III, and IV individuals. Age category I, not shown, is the same as shown for category II, except that M^3 is not fully erupted.

NONGEOGRAPHIC VARIATION

The kinds of nongeographic variation considered in the study include secondary sexual, age, and individual variation. Individuals were first sorted by sex and age and tested for nongeographic variation with samples maintained in separate age and sex categories (Straney, 1978). This method should keep separate the effect of age and sex upon nongeographic variation. Then, in the absence of significant secondary sexual variation in each age category, the sexes were combined in the geographic samples used for the analysis of age variation.

Secondary Sexual Variation

Specimens from selected populations of *Steatomys cuppedius* and *S. caurinus* were assigned to one of four age categories (see section on Age Variation for details of ageing method and criteria). *Steatomys cuppedius* males and females of age categories II and III from Panisau, Nigeria, and age category II from Senegal were tested for significant differences in size. Similar tests between various

ages of samples of male and female *S. caurinus* from Pirisi, Ghana (age II and III); Gudi, Nigeria (age III); and Cella, Upper Volta (age II) were performed. These samples were tested as only those populations and age categories from which sufficient individuals of both sexes were available could be analyzed.

The results of these tests on age category II individuals of *S. cuppedius* from Panisau, Nigeria, and of *S. caurinus* from Pirisi, Ghana, are shown in Table 1, whereas the results for age category III of the same geographic samples are listed in Table 2. The data for the other comparisons given above are not presented but are on file in the Section of Mammals, Carnegie Museum of Natural History.

Steatomys caurinus.—No significant differences in measurements between 16 males and 20 females from Gudi, Nigeria (age III), 13 males and 14 females from Cella, Upper Volta (age II), and 14 males and nine females from Pirisi, Ghana (age II) were found. The results of the latter comparison are

Table 1.—Secondary sexual variation in external and cranial measurements of age category II specimens of *Steatomys caurinus* from Pirisi, Ghana, and *S. cuppedius* from Panisau, Nigeria. Means for males and females that are significantly different at the 5% level are marked with an asterisk.

Measurements and sex	N	Mean \pm 2 SE	Range	CV
<i>Steatomys caurinus</i>				
Total length				
Male	11	139.4 \pm 5.38	130–156	6.4
Female	9	133.4 \pm 4.10	128–147	4.6
Length of tail				
Male	11	38.8 \pm 1.54	34–41	6.6
Female	9	39.4 \pm 2.16	35–46	8.2
Length of hindfoot				
Male	11	19.0 \pm 0.38	18–20	3.3
Female	9	18.4 \pm 0.59	17–20	4.8
Length of ear				
Male	11	16.3 \pm 0.55	15–18	5.6
Female	9	15.8 \pm 0.44	15–17	4.2
Weight				
Male	11	34.4 \pm 7.40	19–60	35.7
Female	9	32.2 \pm 4.73	22–47	22.0
Greatest length of skull				
Male	8	24.4 \pm 0.54	23.4–25.7	3.1
Female	4	23.7 \pm 0.46	23.2–24.2	1.9
Condylbasal length				
Male	7	23.2 \pm 0.46	22.5–24.3	2.6
Female	6	22.7 \pm 0.53	22.0–23.4	2.8
Zygomatic breadth				
Male	8	12.1 \pm 0.28	11.4–12.6	3.3
Female	3	11.8 \pm 0.35	11.5–12.1	2.5
Interorbital breadth				
Male	11	3.8 \pm 0.09	3.7–4.1	4.1
Female	8	3.8 \pm 0.14	3.6–4.1	5.1
Rostral breadth				
Male	11	4.5 \pm 0.10	4.3–4.8	3.5
Female	9	4.3 \pm 0.15	4.0–4.7	5.1
Oblique length of bulla				
Male	7	5.4 \pm 0.11	5.1–5.5	2.8
Female	4	5.3 \pm 0.19	5.1–5.5	3.6
Greatest length of bulla				
Male	7	8.0 \pm 0.18	7.8–8.4	3.0
Female	3	8.2 \pm 0.07	8.1–8.2	0.7
Length of maxillary toothrow				
Male	10	4.1 \pm 0.13	3.8–4.4	5.0
Female	9	3.9 \pm 0.09	3.6–4.1	3.6
Breadth across upper molars				
Male	11	5.6 \pm 0.10	5.4–5.9	2.9
Female	9	5.5 \pm 0.14	5.3–5.9	3.7

Table 1.—Continued

Measurements and sex	N	Mean \pm 2 SE	Range	CV
Length of anterior palatal foramen				
Male	11	4.7 \pm 0.14	4.2–5.2	4.9
Female	9	4.6 \pm 0.19	3.9–4.9	6.2
Length of posterior palatal foramen				
Male	10	0.4 \pm 0.07	0.2–0.5	24.6
Female	9	0.4 \pm 0.06	0.3–0.6	20.0
Length of diastema				
Male	11	6.5 \pm 0.19	5.9–7.0	4.8
Female	8	6.2 \pm 0.20	5.7–6.5	4.6
Height of skull				
Male	6	8.7 \pm 0.23	8.4–9.1	3.3
Female	5	8.5 \pm 0.24	8.3–9.0	3.2
Length of mandibular toothrow				
Male	11	3.5 \pm 0.12	3.2–3.9	5.9
Female	9	3.4 \pm 0.14	3.0–3.7	6.2
<i>Steatomys cuppedius</i>				
Total length				
Male	24	109.7 \pm 3.5	97–129	3.5
Female	9	106.3 \pm 4.3	94–112	4.3
Length of tail				
Male	24	42.8 \pm 1.4	38–50	8.0
Female	8	42.1 \pm 1.9	37–45	6.3
Length of hindfoot				
Male	24	15.9 \pm 0.18	15–17	2.8
Female	9	15.6 \pm 0.48	14–16	4.7
Length of ear				
Male	24	12.7 \pm 0.22	12–14	4.3
Female	9	12.4 \pm 0.35	12–13	4.2
Weight				
Male	24	9.4 \pm 0.90	6–14	23.4
Female	9	8.7 \pm 1.25	5–10	21.6
Greatest length of skull				
Male	20	19.7 \pm 0.30	18.4–21.4	3.5
Female	8	19.2 \pm 0.63	17.5–20.3	4.6
Condylbasal length				
Male	21	18.5 \pm 0.30	17.5–20.0	3.8
Female	8	18.0 \pm 0.58	16.4–18.9	4.6
Zygomatic breadth				
Male	23	10.8 \pm 0.14	10.3–11.5	3.0
Female	9	10.8 \pm 0.26	10.2–11.5	3.5
Interorbital breadth				
Male	24	3.6 \pm 0.05	3.3–3.9	3.6
Female	9	3.7 \pm 0.08	3.5–3.9	3.4
Rostral breadth				
Male	24	3.7 \pm 0.08	3.3–4.1	5.6
Female	9	3.7 \pm 0.12	3.5–3.9	4.6

Table 1.—Continued

Measurements and sex	N	Mean \pm 2 SE	Range	CV
Oblique length of bulla				
Male	17	4.5 \pm 0.09	4.2–4.9	4.0
Female	6	4.5 \pm 0.25	4.0–4.9	6.9
Greatest length of bulla				
Male	15	6.8 \pm 0.13	6.4–7.3	3.8
Female	6	6.7 \pm 0.26	6.2–7.1	4.8
Length of maxillary toothrow				
Male	23	3.6 \pm 0.07	3.3–4.0	4.8
Female	9	3.7 \pm 0.12	3.4–3.9	5.1
Breadth across upper molars				
Male	24	4.9 \pm 0.09	4.4–5.6	4.6
Female	9	4.9 \pm 0.13	4.6–5.2	4.0
Length of anterior palatal foramen				
Male	23	3.7 \pm 0.09	3.1–4.0	5.6
Female	9	3.6 \pm 0.19	3.2–4.2	8.2
Length of posterior palatal foramen*				
Male	22	0.4 \pm 0.03	0.3–0.5	18.3
Female	9	0.5 \pm 0.05	0.4–0.6	15.9
Length of diastema*				
Male	24	4.6 \pm 0.10	4.1–5.0	5.3
Female	9	4.3 \pm 0.05	4.2–4.4	1.8
Height of skull				
Male	18	7.6 \pm 0.10	7.2–7.9	2.8
Female	6	7.5 \pm 0.16	7.2–7.7	2.6
Length of mandibular toothrow				
Male	22	3.1 \pm 0.06	2.9–3.4	4.3
Female	9	3.1 \pm 0.13	2.7–3.3	6.4

given in Table 1. In age category III, individuals from Pirisi, Ghana, females were found to be significantly larger than males only in rostral breadth (Table 2).

Steatomys cuppedius.—No significant differences in size between 17 males and nine females of age category II from Senegal were found. However, in age category II from Panisau, Nigeria, the length of the posterior palatal foramen was larger in females, whereas the length of diastema was larger in males (Table 1). In the population from Panisau, Nigeria, males and females of age category III were found not to differ significantly in size (Table 2).

Conclusions.—No significant differences in size between males and females are obvious. From the comparisons of sexes of two age categories from five geographic samples, only two cranial measure-

Table 2.—Secondary sexual variation in external and cranial measurements of age category III specimens of *Steatomys caurinus* from Pirisi, Ghana, and *S. cuppedius* from Panisau, Nigeria. Significance levels are the same as for Table 1.

Measurements and sex	N	Mean \pm 2 SE	Range	CV
<i>Steatomys caurinus</i>				
Total length				
Male	14	158.2 \pm 4.59	137–169	5.4
Female	7	157.6 \pm 5.70	145–165	4.8
Length of tail				
Male	14	43.1 \pm 3.15	36–59	13.7
Female	7	41.4 \pm 2.65	36–46	8.5
Length of hindfoot				
Male	14	19.7 \pm 0.39	18–21	3.7
Female	7	19.6 \pm 0.40	19–20	2.7
Length of ear				
Male	14	17.2 \pm 0.43	16–18	4.7
Female	7	17.1 \pm 0.68	16–18	5.2
Weight				
Male	14	54.4 \pm 5.08	37–68	17.5
Female	7	53.3 \pm 8.31	34–66	20.6
Greatest length of skull				
Male	12	26.4 \pm 0.47	24.9–27.8	3.1
Female	5	26.3 \pm 0.78	25.6–27.6	3.3
Condylolbasal length				
Male	12	25.3 \pm 0.53	23.5–26.6	3.6
Female	5	25.3 \pm 0.63	24.7–26.4	2.8
Zygomatic breadth				
Male	12	12.9 \pm 0.22	12.2–13.4	3.0
Female	4	13.0 \pm 0.43	12.7–13.6	3.3
Interorbital breadth				
Male	14	3.9 \pm 0.10	3.6–4.2	4.7
Female	6	3.9 \pm 0.17	3.6–4.2	5.2
Rostral breadth*				
Male	14	4.8 \pm 0.13	4.4–5.1	5.2
Female	7	5.0 \pm 0.17	4.7–5.3	4.4
Oblique length of bulla				
Male	13	5.8 \pm 0.12	5.5–6.3	3.7
Female	4	6.0 \pm 0.17	5.8–6.2	2.9
Greatest length of bulla				
Male	10	8.8 \pm 0.21	8.4–9.2	3.8
Female	5	8.8 \pm 0.17	8.5–9.0	2.2
Length of maxillary toothrow				
Male	14	4.0 \pm 0.09	3.7–4.3	4.1
Female	7	4.1 \pm 0.17	3.8–4.4	5.6
Breadth across upper molars				
Male	14	5.9 \pm 0.11	5.6–6.2	3.5
Female	7	6.1 \pm 0.17	5.8–6.4	3.8

Table 2.—Continued

Measurements and sex	N	Mean \pm 2 SE	Range	CV
Length of anterior palatal foramen				
Male	14	5.0 \pm 0.11	4.7–5.4	4.0
Female	7	5.2 \pm 0.24	4.7–5.6	6.2
Length of posterior palatal foramen				
Male	14	0.5 \pm 0.09	0.3–0.8	31.0
Female	7	0.6 \pm 0.16	0.3–1.0	38.6
Length of diastema				
Male	14	7.2 \pm 0.19	6.5–7.8	4.9
Female	7	7.3 \pm 0.22	7.0–7.7	4.0
Height of skull				
Male	10	9.2 \pm 0.25	8.4–9.7	4.3
Female	4	9.3 \pm 0.25	9.0–9.5	2.6
Length of mandibular toothrow				
Male	13	3.5 \pm 0.13	3.1–3.9	6.8
Female	7	3.4 \pm 0.13	3.2–3.7	5.0
<i>Steatomys cuppedius</i>				
Total length				
Male	8	118.3 \pm 5.82	107–133	7.0
Female	8	117.9 \pm 4.86	105–125	5.8
Length of tail				
Male	8	44.0 \pm 2.98	39–52	9.6
Female	8	43.3 \pm 2.67	37–48	8.7
Length of hindfoot				
Male	8	16.0 \pm 0.38	15–17	3.3
Female	8	16.0 \pm 0.53	15–17	4.7
Length of ear				
Male	8	13.5 \pm 0.38	13–14	4.0
Female	8	12.9 \pm 0.59	12–14	6.5
Weight				
Male	8	12.1 \pm 2.08	8–17	24.3
Female	8	13.3 \pm 1.55	10–17	16.5
Greatest length of skull				
Male	8	20.5 \pm 0.47	19.6–21.4	3.2
Female	8	20.8 \pm 0.41	20.1–21.6	2.8
Condylbasal length				
Male	8	19.4 \pm 0.51	18.1–20.2	3.7
Female	8	19.6 \pm 0.37	19.1–20.6	2.7
Zygomatic breadth				
Male	8	11.1 \pm 0.26	10.5–11.5	3.4
Female	8	11.3 \pm 0.25	10.7–11.8	3.2
Interorbital breadth				
Male	8	3.6 \pm 0.13	3.4–4.0	5.1
Female	8	3.7 \pm 0.07	3.6–3.8	2.7
Rostral breadth				
Male	8	3.9 \pm 0.14	3.6–4.1	4.9
Female	8	3.9 \pm 0.14	3.7–4.3	5.0

Table 2.—Continued

Measurements and sex	N	Mean \pm 2 SE	Range	CV
Oblique length of bulla				
Male	6	4.7 \pm 0.08	4.5–4.8	2.2
Female	8	4.7 \pm 0.08	4.5–4.8	2.5
Greatest length of bulla				
Male	6	7.0 \pm 0.12	6.7–7.1	2.2
Female	7	7.1 \pm 0.26	6.4–7.4	4.8
Length of maxillary toothrow				
Male	8	3.6 \pm 0.10	3.4–3.9	4.1
Female	8	3.7 \pm 0.13	3.5–4.0	4.9
Breadth across upper molars				
Male	8	5.1 \pm 0.16	4.6–5.3	4.4
Female	8	5.1 \pm 0.12	4.9–5.4	3.4
Length of anterior palatal foramen				
Male	8	4.0 \pm 0.24	3.4–4.4	8.5
Female	8	3.9 \pm 0.15	3.5–4.2	5.4
Length of posterior palatal foramen				
Male	7	0.4 \pm 0.07	0.3–0.5	21.7
Female	8	0.4 \pm 0.05	0.3–0.5	18.9
Length of diastema				
Male	8	5.0 \pm 0.14	4.7–5.2	4.0
Female	8	4.9 \pm 0.12	4.6–5.1	3.4
Height of skull				
Male	6	7.8 \pm 0.16	7.6–8.1	2.5
Female	8	7.8 \pm 0.19	7.5–8.2	3.4
Length of mandibular toothrow				
Male	8	3.1 \pm 0.11	2.7–3.2	5.2
Female	8	3.1 \pm 0.10	2.9–3.3	4.4

ments were found to be significantly different—in individuals of *S. cuppedius* from Panisau, Nigeria. Therefore, in all subsequent analyses the sexes were pooled.

Age Variation

Age categories used in this study are shown in Fig. 1; these categories are usually referred to as follows: Age I, juveniles; Age II, subadults; Age III, young adults; Age IV, adults. Age I is not illustrated in Fig. 1; M³ in this age category has not erupted fully. These categories are arbitrary, based on dental wear, and do not reflect reproductive age. *Steatomys cuppedius* populations tested for age variation are the Senegal population, which had sufficient sample sizes in categories I, II, and III, and the Panisau, Nigeria, sample, which had adequate numbers in categories I, III, and IV. Those

Table 3.—Variation with age in external and cranial measurements of *Steatomys caurinus* from Yama, Ivory Coast, and *S. cuppedius* from Panisau, Nigeria. Age classes are listed in decreasing order from the largest mean. Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 5% level. Groups of means of nonsignificant differences are labelled "ns."

Measurements and age classes	N	Mean \pm 2 SE	Range	CV	SS-STP
<i>Steatomys caurinus</i>					
Total length					
IV	10	166.8 \pm 8.00	155–200	7.5	
III	13	147.8 \pm 6.54	134–169	8.0	
II	14	135.3 \pm 2.64	121–156	6.5	
Length of tail					
IV	10	52.7 \pm 3.94	45–64	11.8	
III	13	45.7 \pm 3.16	38–58	12.5	
II	44	44.1 \pm 1.55	35–55	11.7	
Length of hindfoot					
IV	10	19.0 \pm 0.73	17–21	6.1	ns
III	13	18.8 \pm 0.51	18–20	4.9	
II	44	18.5 \pm 0.25	17–20	4.4	
Length of ear					
IV	10	18.1 \pm 0.55	17–20	4.8	
III	13	17.7 \pm 0.53	16–20	5.4	
II	44	16.7 \pm 0.27	15–19	5.3	
Weight					
IV	10	41.8 \pm 4.66	35–58	17.6	
III	13	32.0 \pm 6.38	22–54	35.9	
II	14	22.7 \pm 1.86	12–38	27.2	
Greatest length of skull					
IV	0				
III	4	25.4 \pm 1.14	24.3–26.5	4.5	
II	11	23.7 \pm 0.35	22.7–24.6	2.4	
Condylbasal length					
IV	5	25.8 \pm 0.79	24.6–26.7	3.4	
III	9	23.9 \pm 0.63	22.8–25.3	4.0	
II	29	22.7 \pm 0.33	20.8–23.9	3.9	
Zygomatic breadth					
IV	4	13.2 \pm 0.24	12.9–13.4	1.8	
III	7	12.3 \pm 0.53	11.3–13.0	5.7	
II	23	11.7 \pm 0.20	10.7–12.5	4.1	
Interorbital breadth					
IV	9	4.1 \pm 0.07	3.9–4.2	2.5	
III	12	3.9 \pm 0.07	3.6–4.1	3.3	
II	38	3.8 \pm 0.05	3.4–4.1	4.4	
Rostral breadth					
IV	9	5.1 \pm 0.15	4.9–5.5	4.3	
III	13	4.4 \pm 0.11	4.1–4.7	4.5	
II	39	4.2 \pm 0.06	3.9–4.6	4.3	

Table 3.—Continued.

Measurements and age classes	N	Mean \pm 2 SE	Range	CV	SS- STP
Oblique length of bulla					
IV	7	5.8 \pm 0.24	5.3–6.1	5.6	
III	10	5.4 \pm 0.15	4.9–5.7	4.3	
II	34	5.3 \pm 0.08	4.8–5.7	4.2	
Greatest length of bulla					
IV	6	9.0 \pm 0.33	8.6–9.5	4.5	
III	8	8.4 \pm 0.18	8.0–8.8	3.1	
II	31	8.2 \pm 0.09	7.7–8.7	3.2	
Length of maxillary toothrow					
IV	10	4.1 \pm 0.14	3.7–4.4	5.5	ns
III	13	4.1 \pm 0.10	3.8–4.4	4.3	
II	42	4.0 \pm 0.05	3.6–4.4	4.0	
Breadth across upper molars					
IV	8	6.1 \pm 0.16	5.8–6.5	3.8	
III	12	5.7 \pm 0.10	5.4–6.1	3.1	
II	37	5.5 \pm 0.07	5.1–6.1	3.6	
Length of anterior palatal foramen					
IV	9	5.6 \pm 0.13	5.3–5.9	3.4	
III	12	4.9 \pm 0.19	4.4–5.4	6.7	
II	37	4.6 \pm 0.11	4.2–5.9	7.1	
Length of posterior palatal foramen					
IV	7	0.5 \pm 0.10	0.3–0.7	26.2	ns
III	11	0.5 \pm 0.07	0.3–0.7	23.1	
II	32	0.5 \pm 0.04	0.3–0.7	24.3	
Length of diastema					
IV	9	7.2 \pm 0.24	6.8–8.0	5.0	
III	13	6.3 \pm 0.30	5.6–7.4	8.7	
II	40	6.0 \pm 0.10	5.2–6.6	5.4	
Height of skull					
IV	4	9.6 \pm 0.15	9.5–9.8	1.6	
III	9	9.0 \pm 0.23	8.6–9.7	3.9	
II	26	8.7 \pm 0.10	8.3–9.1	3.0	
Length of mandibular toothrow					
IV	10	3.6 \pm 0.18	3.1–4.1	8.1	ns
III	13	3.5 \pm 0.08	3.2–3.7	4.3	
II	43	3.5 \pm 0.05	3.2–3.9	4.9	
<i>Steatomys cuppedius</i>					
Total length					
IV	6	132.7 \pm 7.04	120–143	6.5	
III	16	118.1 \pm 3.66	105–133	6.2	
II	33	108.8 \pm 2.85	94–129	7.5	
Length of tail					
IV	6	48.7 \pm 2.29	46–54	5.8	
III	16	43.6 \pm 1.94	37–52	8.9	
II	32	42.6 \pm 1.14	37–50	7.5	
Length of hindfoot					
IV	6	16.0 \pm 0.52	15–17	4.0	ns
III	16	16.0 \pm 0.32	15–17	4.0	
II	33	15.8 \pm 0.19	14–17	3.5	

Table 3.—Continued.

Measurements and age classes	N	Mean \pm 2 SE	Range	CV	SS- STP
Length of ear					
IV	6	13.7 \pm 0.42	13–14	3.8	
III	16	13.2 \pm 0.38	12–14	5.7	
II	33	12.6 \pm 0.19	12–14	4.3	
Weight					
IV	6	16.2 \pm 2.75	13–22	20.9	
III	16	12.7 \pm 1.29	8–17	20.3	
II	33	9.2 \pm 0.74	5–14	23.0	
Greatest length of skull					
IV	5	22.4 \pm 0.88	21.3–23.9	4.4	
III	16	20.7 \pm 0.31	19.6–21.6	3.0	
II	28	19.5 \pm 0.29	17.5–21.4	3.9	
Condylobasal length					
IV	6	21.0 \pm 0.76	20.1–22.5	4.5	
III	16	19.5 \pm 0.31	18.1–20.6	3.2	
II	29	18.3 \pm 0.28	16.4–20.0	4.1	
Zygomatic breadth					
IV	6	11.8 \pm 0.38	11.2–12.4	4.0	
III	16	11.2 \pm 0.19	10.5–11.8	3.4	
II	32	10.8 \pm 0.12	10.2–11.5	3.1	
Interorbital breadth					
IV	6	3.9 \pm 0.16	3.6–4.1	5.0	
III	16	3.7 \pm 0.07	3.4–4.0	4.0	
II	33	3.6 \pm 0.05	3.3–3.9	3.6	
Rostral breadth					
IV	6	4.2 \pm 0.24	3.9–4.7	6.9	
III	16	3.9 \pm 0.09	3.6–4.3	4.8	
II	33	3.7 \pm 0.07	3.3–4.1	5.3	
Oblique length of bulla					
IV	5	4.8 \pm 0.23	4.4–5.0	5.3	
III	14	4.7 \pm 0.06	4.5–4.8	2.3	
II	23	4.5 \pm 0.09	4.0–4.9	4.7	
Greatest length of bulla					
IV	5	7.4 \pm 0.19	7.1–7.7	2.9	
III	13	7.1 \pm 0.15	6.4–7.4	4.0	
II	21	6.8 \pm 0.12	6.2–7.3	4.0	
Length of maxillary toothrow					
IV	6	3.8 \pm 0.12	3.6–4.0	3.9	ns
III	16	3.7 \pm 0.09	3.4–4.0	4.7	
II	32	3.6 \pm 0.06	3.3–4.0	4.9	
Breadth across upper molars					
IV	6	5.3 \pm 0.19	5.1–5.7	4.4	
III	16	5.1 \pm 0.10	4.6–5.4	3.8	
II	33	4.9 \pm 0.07	4.4–5.6	4.3	
Length of anterior palatal foramen					
IV	6	4.2 \pm 0.18	4.0–4.6	5.3	
III	16	4.0 \pm 0.14	3.4–4.4	6.9	
II	32	3.7 \pm 0.08	3.1–4.2	6.5	

Table 3.—Continued.

Measurements and age classes	N	Mean \pm 2 SE	Range	CV	SS- STP
Length of posterior palatal foramen					
IV	6	0.4 \pm 0.08	0.3–0.5	20.4	ns
III	15	0.4 \pm 0.04	0.3–0.5	20.3	
II	31	0.4 \pm 0.03	0.3–0.6	18.5	
Length of diastema					
IV	6	5.3 \pm 0.35	4.8–5.9	8.0	
III	16	5.0 \pm 0.09	4.6–5.2	3.8	
II	33	4.5 \pm 0.08	4.1–5.0	5.4	
Height of skull					
IV	6	8.2 \pm 0.18	8.0–8.5	2.7	
III	14	7.8 \pm 0.12	7.5–8.2	2.9	
II	24	7.6 \pm 0.08	7.2–7.9	2.7	
Length of mandibular toothrow					
IV	6	3.4 \pm 0.12	3.2–3.6	4.5	
III	16	3.1 \pm 0.07	2.7–3.3	4.7	
II	31	3.1 \pm 0.05	2.7–3.4	4.9	

populations of *S. caurinus* tested were from Yama, Ivory Coast, with sufficient individuals of categories II, III, and IV; Pirisi, Ghana (II and III); Gudi, Nigeria (II and III); and Cella, Upper Volta (II and III). For each of the 19 external and cranial measurements, samples of combined sexes were tested to determine if the differences between the means of the age categories were significantly different ($P \leq 0.05$). If found to be significantly different, the Sum of Squares Simultaneous Test Procedure was used to find maximally nonsignificant subsets. The results of these tests in *S. cuppedius* from Panisau, Nigeria (age II, III, IV), and *S. caurinus* from Yama, Ivory Coast (age II, III, IV), are presented (Table 3).

Steatomys caurinus.—In the population from Yama, Ivory Coast, nonoverlapping subsets among age categories II, III, and IV were found in six (total length, weight, condylbasal length, rostral breadth, diastemal length, and height of skull) of 19 measurements; no greatest length of skull measurements are available for age category IV in this sample. Little or no variation in age exists in the following measurements: length of hindfoot; interorbital breadth; lengths of maxillary toothrow; posterior palatal foramen; mandibular toothrow. A similar trend was found in the other populations of *S. caurinus* tested but is not presented in tabular form.

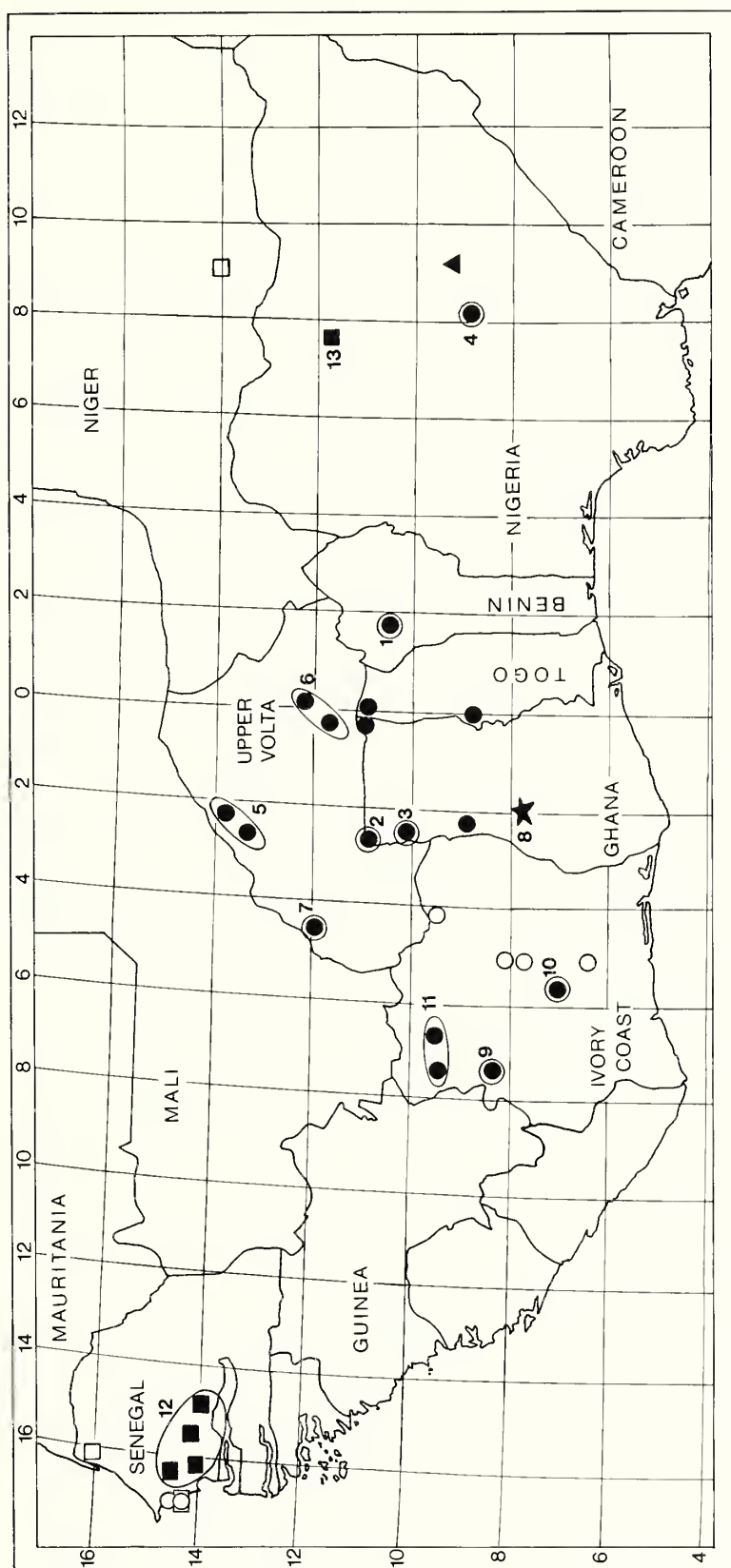


Fig. 2.—Distribution of West African taxa of *Steatomys* showing type localities for each taxon, literature records and specimens examined. OTUs are designated, with inclusive individual localities, by numbers. See text for list of localities included in each OTU. Solid symbols represent localities of specimens examined; open symbols represent localities of literature records. Solid star represents type locality of *S. jacksoni*. Solid triangle represents type locality of *S. caurinus*; the remaining localities of this species are represented by solid or open circles. Solid square indicating OTU 13 represents the type locality of *S. cuppedius*; the remaining localities of this species are represented by solid or open squares. Both *S. caurinus* and *S. cuppedius* are reported from M'Bour, Senegal.

Steatomys cuppedius.—Three nonoverlapping subsets among age categories II, III, and IV in nine (total length, weight, greatest length of skull, condylobasal length, zygomatic breadth, rostral breadth, greatest length of bulla, length of diastema, and height of skull) of 19 measurements were found in the population from Panisau, Nigeria (Table 3). Three characters (lengths of hindfoot, maxillary toothrow, and anterior palatal foramen) showed no significant differences among the different age categories tested. In comparing measurements from the different age categories (I, II, and III) in the population from Senegal, a similar trend emerges, although it is not presented in tabular form.

Conclusions.—From these results, it is apparent that none of the age categories can be pooled in either species for a study of geographic variation. It would be ideal if age IV (adult) specimens could be used for a study of geographic variation in these species. However, due to a lack of sufficient samples of age IV specimens, only specimens belonging to age category III were used.

Individual Variation

The majority of measurements examined revealed a relatively low degree of individual variation as expressed by the coefficient of variation. External measurements were generally more variable than the cranial measurements (Tables 1, 2, 3). This was, however, not as pronounced in *Steatomys cuppedius* as in *Steatomys caurinus*. Of external measurements, weight showed the most variation, with coefficients of variation above 20. Cranial measurements in both species usually had coefficients of variation of less than 5, except in length of posterior palatal foramen where these values usually were above 15.

Conclusions.—Due to the tendency of the external measurements, especially weight, to show relatively higher individual variation expressed as coefficients of variation than did the cranial measurements, all external measurements were excluded from the multivariate analyses of geographic variation. Of the cranial measurements, length of posterior palatal foramen was excluded from this analysis due to its high level of individual variation.

RELATIONSHIPS OF SPECIES

All individuals from West Africa of age category III, and a few specimens that were borderline between category III and IV in age, were grouped into 13 geographic samples. These geographic samples (OTUs) are as follows (see also Fig. 2): 1) Kouande, Benin; 2) Bangwon, Ghana; 3) Pirisi, Ghana; 4) Gudi, Nigeria; 5) Dio and Barga, Upper Volta; 6) Cella and Nayoure, Upper Volta; 7) Fo, Upper Volta; 8) Wenchi, Ghana; 9) Tyenko, Ivory Coast; 10) Diali, Ivory Coast; 11) Sienso and Yama, Ivory Coast; 12) Diourbel, Kaffrine, Kaolack and Koughoul, Senegal; and 13) Panisau, Nigeria.

Steatomys caurinus was described by Thomas (1912) as being generally brownish fawn, but with a darker mid-dorsal area and more distinct color along the sides of the belly. Rosevear (1969) summarized the color of *S. caurinus* as being "medium warm reddish brown" (the tips of the hair were warm brown and the bases were dark gray). According to the description by Hayman (1936), the dorsal pelage of *S. jacksoni* is plumbeous drab in color, with the flanks slightly paler, whereas Rosevear (1969) describes this species as being dark brownish-gray in color of pelage. A large number

of the specimens examined in the present study have skins soiled by residual fats and oils, making an accurate definition of an already variable character, color of pelage, difficult. The dorsal pelage color of *S. cuppedius* was described originally by Thomas and Hinton (1920) as being pale drab with pale sides, and more recently by Rosevear (1969) as being pale, slightly sandy gray. Specimens of this species generally did not have soiled skins such as was found for *S. caurinus*.

Hayman (1936) stated in the original description of *S. jacksoni* that the braincase of the holotype was not sharply truncated as in other species of the genus he had examined, and that the interparietal was lengthened from front to back and noticeably widened anteroposteriorly in the middle part. We have found in the present study that the older animals, such as age category IV individuals, exhibit relatively less truncated skulls than do the younger animals. Hayman (1936) gave a length of 4.5 mm for the interparietal of *S. jacksoni* as compared to 2.5 mm in *S. caurinus*. The length of the interparietal bone of all specimens examined in the present study, with the exception of the holotype of *S. jacksoni*

Table 4.—*Geographic variation in external and cranial measurements of age category III individuals among 10 geographic samples (OTUs) of Steatomys caurinus and two geographic samples of S. cuppedius. Results of ANOVA analysis indicating significance at the 5% level for S. cuppedius are indicated by an asterisk next to the character heading. See Fig. 2 and text for key to localities included in each OTU.*

Sam- ple	N	Mean \pm 2 SE	Range	CV
<i>Steatomys caurinus</i>				
Total length				
1	1	167.0		
2	2	129.0	121–137	
3	21	158.0 \pm 3.52	137–169	5.1
4	36	159.2 \pm 3.93	126–178	7.4
5	2	142.5	142–143	
6	18	161.2 \pm 5.82	136–178	7.7
7	1	154.0		
9	5	164.4 \pm 9.11	149–173	6.2
10	3	168.7 \pm 27.1	142–186	13.9
11	15	148.6 \pm 6.48	134–169	8.4
Length of tail				
1	1	48.0		
2	2	37.0	35–39	
3	21	42.5 \pm 2.26	36–59	12.2
4	36	45.9 \pm 0.21	37–52	7.9
5	2	40.0	38–42	
6	18	45.8 \pm 2.09	40–53	9.7
7	1	51.0		
9	5	55.4 \pm 3.2	50–59	6.5
10	3	59.0 \pm 12.5	47–68	18.3
11	15	46.6 \pm 3.33	38–60	13.8
Length of hindfoot				
1	1	18.0		
2	2	17.5	17–18	
3	21	19.7 \pm 0.29	18–21	3.3
4	36	19.7 \pm 0.21	18–21	3.2
5	2	19.0	19	
6	18	18.8 \pm 0.50	17–21	5.6
7	1	18.0		
9	5	19.0 \pm 1.10	17–20	6.4
10	3	19.0 \pm 1.15	18–20	5.3
11	15	18.7 \pm 0.46	18–20	4.7
Length of ear				
1	1	16.0		
2	2	15.5	15–16	
3	21	17.2 \pm 0.36	16–18	4.7
4	36	17.6 \pm 0.36	15–20	6.1
5	2	15.0	15	
6	18	17.1 \pm 0.57	14–19	7.1
7	1	18.0		
9	5	17.4 \pm 0.49	17–18	3.4
10	3	18.0 \pm 2.0	16–19	9.6
11	15	17.7 \pm 0.54	16–20	5.9
Weight				
1	1	28.0		
2	2	31.5	26–37	
3	21	54.0 \pm 4.26	34–68	18.1

Table 4.—*Continued.*

Sam- ple	N	Mean \pm 2 SE	Range	CV
4	35	48.2 \pm 3.56	25–68	21.9
5	2	30.5	30–31	
6	18	48.4 \pm 5.35	23–70	23.4
7	1	17.0		
9	5	39.6 \pm 7.71	32–53	21.8
10	3	51.3 \pm 24.0	29–70	40.4
11	15	31.7 \pm 5.59	22–54	34.2
Greatest length of skull				
1	1	—		
2	2	—		
3	17	26.4 \pm 0.39	24.9–27.8	3.1
4	32	26.6 \pm 0.38	24.2–28.4	4.0
5	1	23.7		
6	9	26.6 \pm 0.72	24.3–28.0	4.1
7	1	25.5		
9	2	27.6 \pm 1.00	27.1–28.1	2.6
10	3	—		
11	5	25.2 \pm 1.03	24.1–26.5	4.6
Condylolbasal length				
1	1	—		
2	2	—		
3	17	25.3 \pm 0.41	23.4–26.6	3.3
4	26	25.3 \pm 0.37	23.1–27.0	3.7
5	2	23.0	22.6–23.4	
6	10	25.3 \pm 0.87	22.8–27.0	5.5
7	1	24.2		
9	5	25.6 \pm 1.05	23.8–27.0	4.6
10	3	25.7 \pm 2.60	23.2–27.5	8.8
11	11	23.9 \pm 0.68	22.5–25.8	4.7
Zygomatic breadth				
1	1	—		
2	2	—		
3	16	13.0 \pm 0.19	12.2–13.6	3.0
4	22	13.1 \pm 0.23	12.2–13.8	4.1
5	1	12.0		
6	12	12.8 \pm 0.31	12.0–13.6	4.2
7	1	12.4		
9	5	13.1 \pm 0.61	12.1–13.8	5.2
10	3	13.5 \pm 0.98	12.5–14.1	6.3
11	9	12.3 \pm 0.51	11.3–13.5	6.2
Interorbital breadth				
1	1	—		
2	1	3.5		
3	20	3.9 \pm 0.08	3.6–4.2	4.7
4	34	3.9 \pm 0.06	3.5–4.3	4.1
5	2	3.9	3.9	
6	18	3.9 \pm 0.06	3.7–4.1	3.1
7	1	3.9		
9	5	4.2 \pm 0.19	3.8–4.3	5.0
10	3	4.0 \pm 0.29	3.8–4.3	6.2
11	14	3.9 \pm 0.09	3.6–4.3	4.4
Rostral breadth				
1	1	—		
2	2	4.1	4.0–4.2	
3	21	4.8 \pm 0.12	4.4–5.3	5.5

Table 4.—Continued.

Sam- ple	N	Mean \pm 2 SE	Range	CV
4	35	4.7 \pm 0.11	3.9–5.3	6.9
5	2	4.4	4.0–4.7	
6	17	4.9 \pm 0.13	4.5–5.4	5.5
7	1	4.6		
9	5	4.8 \pm 0.24	4.4–5.1	5.6
10	3	4.9 \pm 0.58	4.4–5.4	10.3
11	15	4.5 \pm 0.12	4.1–4.9	5.1

Oblique length of bulla

1	1	—		
2	1	5.2		
3	17	5.9 \pm 0.10	5.5–6.3	3.5
4	31	5.8 \pm 0.09	5.2–6.5	4.3
5	2	6.0	5.5–6.5	
6	10	5.9 \pm 0.19	5.6–6.5	5.0
7	1	5.7		
9	5	5.7 \pm 0.24	5.4–6.0	4.8
10	3	6.0 \pm 0.18	5.8–6.1	2.5
11	12	5.4 \pm 0.15	4.9–5.9	4.7

Greatest length of bulla

1	1	—		
2	1	8.0		
3	15	8.8 \pm 0.15	8.4–9.2	3.3
4	30	9.0 \pm 0.13	8.0–9.7	3.8
5	2	8.2	8.0–8.3	
6	9	8.7 \pm 0.21	8.2–9.3	3.6
7	1	8.5		
9	5	9.0 \pm 0.55	8.1–9.6	6.8
10	3	9.0 \pm 0.80	8.8–9.4	3.8
11	10	8.6 \pm 0.28	8.0–9.6	5.1

Length of maxillary toothrow

1	1	—		
2	2	3.9	3.9	
3	21	4.1 \pm 0.08	3.7–4.4	4.6
4	36	4.2 \pm 0.05	3.8–4.5	3.8
5	2	4.0	3.8–4.1	
6	17	4.3 \pm 0.10	3.9–4.6	4.9
7	1	3.8		
9	5	4.2 \pm 0.12	4.1–4.4	3.1
10	3	4.1 \pm 0.29	3.8–4.3	6.1
11	15	4.1 \pm 0.08	3.8–4.4	4.0

Breadth across upper molars

1	1	—		
2	2	5.5	5.4–5.5	
3	21	5.9 \pm 0.10	5.6–6.4	3.7
4	34	6.0 \pm 0.10	5.0–6.5	4.8
5	2	5.8	5.7–5.8	
6	17	5.9 \pm 0.17	5.1–6.4	5.9
7	1	6.0		
9	5	6.0 \pm 0.19	5.7–6.2	3.6
10	3	6.0 \pm 0.42	5.7–6.4	6.0
11	14	5.7 \pm 0.13	5.4–6.3	4.2

Length of anterior palatal foramen

1	1	—		
2	2	4.3	4.0–4.5	
3	21	5.1 \pm 0.11	4.7–5.6	4.9

Table 4.—Continued.

Sam- ple	N	Mean \pm 2 SE	Range	CV
4	35	4.8 \pm 0.08	4.4–5.2	4.6
5	2	4.3	4.3	
6	13	5.1 \pm 0.21	4.5–5.5	7.4
7	1	5.0		
9	5	5.3 \pm 0.42	4.6–5.9	8.9
10	3	5.2 \pm 0.70	4.6–5.8	11.6
11	14	4.9 \pm 0.17	4.4–5.4	6.5

Length of posterior palatal foramen

1	1	—		
2	2	0.5	0.4–0.5	
3	21	0.5 \pm 0.08	0.3–1.0	33.0
4	30	0.5 \pm 0.04	0.3–0.7	24.2
5	2	0.5	0.5	
6	17	0.6 \pm 0.06	0.4–0.8	17.4
7	1	0.4		
9	5	0.5 \pm 0.07	0.4–0.6	16.1
10	3	0.6 \pm 0.31	0.4–0.9	44.1
11	15	0.5 \pm 0.07	0.3–0.7	23.4

Length of diastema

1	1	—		
2	2	6.2	6.0–6.4	
3	21	7.2 \pm 0.15	6.5–7.8	4.6
4	36	7.0 \pm 0.14	6.0–7.6	5.9
5	2	6.6	6.3–6.8	
6	17	7.0 \pm 0.21	6.3–7.7	6.2
7	1	6.8		
9	5	6.9 \pm 0.34	6.7–7.6	5.5
10	3	7.2 \pm 1.00	6.3–8.0	12.0
11	15	6.3 \pm 0.28	5.8–7.4	5.6

Height of skull

1	1	—		
2	2	—		
3	14	9.2 \pm 0.19	8.4–9.7	3.8
4	32	9.2 \pm 0.17	7.7–10.1	5.2
5	2	9.2	8.7–9.6	
6	11	9.3 \pm 0.24	8.5–10.0	4.3
7	1	9.1		
9	5	9.6 \pm 0.41	8.9–10.0	4.7
10	3	9.9 \pm 0.77	9.2–10.5	6.7
11	11	9.0 \pm 0.20	8.6–9.2	3.8

Length of mandibular toothrow

1	1	—		
2	2	3.3	3.3	
3	20	3.5 \pm 0.10	3.1–3.9	6.2
4	34	3.5 \pm 0.06	3.1–3.9	5.4
5	2	3.2	3.2	
6	16	3.5 \pm 0.07	3.3–3.8	4.2
7	1	3.2		
9	5	3.5 \pm 0.12	3.3–3.6	3.9
10	3	3.5 \pm 0.29	3.2–3.7	7.2
11	15	3.5 \pm 0.08	3.2–3.7	4.2

Steatomys cuppedius

Total length*

12	5	125.6 \pm 2.58	122–130	2.3
13	16	118.1 \pm 3.66	105–133	6.2

Table 4.—Continued.

Sam- ple	N	Mean \pm 2 SE	Range	CV
Length of tail				
12	5	44.8 \pm 1.60	43–47	4.0
13	16	43.6 \pm 1.94	37–52	8.9
Length of hindfoot				
12	5	15.8 \pm 0.40	15–16	2.8
13	16	16.0 \pm 0.32	15–17	4.0
Length of ear				
12	5	12.8 \pm 0.40	12–13	3.5
13	16	13.2 \pm 0.38	12–14	5.7
Weight*				
12	5	16.8 \pm 5.31	7–23	35.3
13	16	12.7 \pm 1.29	8–17	20.3
Greatest length of skull*				
12	2	22.0 \pm 0.40	21.8–22.2	1.3
13	16	20.7 \pm 0.31	19.6–21.6	3.0
Condylbasal length				
12	3	20.2 \pm 0.35	19.9–20.5	1.5
13	16	19.5 \pm 0.31	18.1–20.6	3.2
Zygomatic breadth				
12	2	11.6 \pm 0.30	11.4–11.7	1.8
13	16	11.2 \pm 0.19	10.5–11.8	3.4
Interorbital breadth				
12	5	3.6 \pm 0.07	3.5–3.7	2.3
13	16	3.7 \pm 0.07	3.4–4.0	4.0
Rostral breadth				
12	5	4.1 \pm 0.14	3.9–4.3	3.9
13	16	3.9 \pm 0.09	3.6–4.3	4.8
Oblique length of bulla*				
12	3	5.1 \pm 0.12	5.0–5.2	2.0
13	14	4.7 \pm 0.06	4.5–4.8	2.3
Greatest length of bulla				
12	2	7.5 \pm 0.10	7.4–7.5	0.9
13	13	7.1 \pm 0.15	6.4–7.4	4.0
Length of maxillary tooththrow				
12	5	3.6 \pm 0.16	3.4–3.9	5.0
13	16	3.7 \pm 0.09	3.4–4.0	4.7
Breadth across upper molars				
12	4	5.1 \pm 0.08	5.0–5.2	1.6
13	16	5.1 \pm 0.10	4.6–5.4	3.8
Length of anterior palatal foramen				
12	3	4.2 \pm 0.07	4.1–4.2	1.4
13	16	4.0 \pm 0.14	3.4–4.4	6.9
Length of posterior palatal foramen				
12	4	0.4 \pm 0.08	0.3–0.5	20.4
13	15	0.4 \pm 0.04	0.3–0.5	20.3
Length of diastema				
12	4	5.1 \pm 0.13	4.9–5.2	2.5
13	16	5.0 \pm 0.09	4.6–5.2	3.8

Table 4.—Continued.

Sam- ple	N	Mean \pm 2 SE	Range	CV
Height of skull				
12	4	8.1 \pm 0.47	7.4–8.4	5.9
13	14	7.8 \pm 0.12	7.5–8.2	2.9
Length of mandibular tooththrow				
12	4	3.2 \pm 0.15	3.1–3.4	4.7
13	16	3.1 \pm 0.07	2.7–3.3	4.7

soni, measured less than 4 mm. The interparietal bones varied in shape from nearly triangular to quadrangular. This variation in shape occurred among specimens within the same age category.

In his original description, Hayman (1936) concluded that *S. jacksoni* was not bigger than *S. caurinus*, but he compared only the external measurements of the two taxa. Thus the single most important character used by Hayman (1936) in describing *S. jacksoni* was the size and shape of the interparietal bone. When the holotype was examined, the interparietal bone did measure 4 mm in length and was clearly longer than any of the other specimens of *Steatomys* examined. Based on this diagnostic character, none of the specimens we examined could be assigned to *S. jacksoni*.

Univariate analysis.—Results of standard univariate statistical analysis for individuals of *Steatomys* from the 13 geographic samples are given in Tables 4 and 5. In age category III specimens (Table 4), there is no overlap in the range of measurements between geographic samples 12 and 13 (*S. cuppedius*) and those of the remainder of the West African geographic samples in four of the 19 characters analyzed (greatest length of skull, condylbasal length, greatest length of bulla, and length of diastema). Comparison of these same analyses for age category IV individuals (Table 5) reveals that 12 of 19 characters (total length, length of ear, weight, greatest length of skull, condylbasal length, zygomatic breadth, rostral breadth, oblique length of bulla, greatest length of bulla, width across upper molars, length of anterior palatal foramen, length of diastema, and height of skull) show no overlap between geographic samples 12 and 13 and the remaining geographic samples analyzed. *Steatomys cuppedius* is readily distinguishable from other West African fat mice in being markedly smaller in size, both externally and cranially, and much paler in color of pelage.

Table 5.—*Geographic variation in external and cranial measurements of age category IV individuals among six geographic samples (OTUs) of Steatomys caurinus and two geographic samples of S. cuppedius. See Fig. 2 and text for key to localities included in each OTU.*

Sam- ple	N	Mean \pm 2 SE	Range	CV
<i>Steatomys caurinus</i>				
Total length				
3	1	155		
4	2	166	162–170	
6	1	179		
9	1	188		
10	1	199		
11	10	166.8 \pm 8.0	155–200	7.5
Length of tail				
3	1	41		
4	2	43	41–45	
6	1	47		
9	1	65		
10	1	—		
11	10	52.7 \pm 3.9	45–64	11.8
Length of hindfoot				
3	1	18.0		
4	2	19.5	19–20	
6	1	18.0		
9	1	20		
10	1	21		
11	10	19.0 \pm 0.73	17–21	6.1
Length of ear				
3	1	17.0		
4	2	17.5	17–18	
6	1	18.0		
9	1	18.0		
10	1	18.0		
11	10	18.1 \pm 0.55	17–20	4.8
Weight				
3	1	56.0		
4	2	55.5	54–57	
6	1	70.0		
9	1	69.0		
10	1	69.0		
11	10	41.8 \pm 4.66	35–58	17.6
Greatest length of skull				
3	1	27.2		
4	1	29.3		
6	0			
9	1	28.5		
10	0			
11	0			
Condylbasal length				
3	1	25.6		
4	1	28.0		
6	1	27.2		
9	1	27.1		
10	1	28.3		
11	5	25.8 \pm 0.79	24.6–26.7	3.4

Table 5.—*Continued.*

Sam- ple	N	Mean \pm 2 SE	Range	CV
Zygomatic breadth				
3	1	13.1		
4	1	15.1		
6	1	13.9		
9	1	14.2		
10	1	14.5		
11	4	13.2 \pm 0.24	12.9–13.4	1.8
Interorbital breadth				
3	1	4.2		
4	2	4.1	3.9–4.2	
6	1	4.1		
9	1	4.0		
10	1	4.2		
11	9	4.1 \pm 0.07	3.9–4.2	2.5
Rostral breadth				
3	1	4.8		
4	2	5.5	5.3–5.6	
6	1	5.5		
9	1	5.3		
10	1	5.4		
11	9	5.1 \pm 0.15	4.9–5.5	4.3
Oblique length of bulla				
3	1	5.8		
4	1	5.9		
6	0			
9	1	6.2		
10	1	6.1		
11	7	5.8 \pm 0.33	8.6–9.5	4.5
Greatest length of bulla				
3	1	9.0		
4	1	9.0		
6	0			
9	1	9.4		
10	1	9.9		
11	6	9.0 \pm 0.33	8.6–9.5	4.5
Length of maxillary toothrow				
3	1	3.9		
4	2	4.5	4.4–4.5	
6	1	4.4		
9	1	4.3		
10	1	3.9		
11	10	4.1 \pm 0.14	3.7–4.4	5.5
Breadth across upper molars				
3	1	6.0		
4	2	6.4	5.9–6.8	
6	1	6.2		
9	1	6.4		
10	1	6.1		
11	8	6.1 \pm 0.16	5.8–6.5	3.8
Length of anterior of anterior palatal foramen				
3	1	5.2		
4	1	5.1		

Table 5.—Continued.

Sam- ple	N	Mean \pm 2 SE	Range	CV
6	1	5.6		
9	1	5.2		
10	1	6.0		
11	9	5.6 \pm 0.13	5.3–5.9	3.4
Length of posterior palatal foramen				
3	1	0.7		
4	2	0.5	0.5	
6	1	0.6		
9	1	0.6		
10	1	0.5		
11	7	0.5 \pm 0.10	0.3–0.7	26.2
Length of diastema				
3	1	7.3		
4	2	7.5	6.9–8.0	
6	1	7.1		
9	1	7.4		
10	1	8.6		
11	9	7.2 \pm 0.24	6.8–8.0	5.0
Height of skull				
3	1	9.3		
4	1	10.6		
6	1	10.1		
9	1	10.5		
10	1	10.1		
11	4	9.6 \pm 0.15	9.5–9.8	1.6
Length of mandibular toothrow				
3	0			
4	2	3.6	3.5–3.6	
6	1	3.8		
9	1	3.7		
10	0			
11	10	3.6 \pm 0.18	3.1–4.1	8.1
<i>Steatomys cuppedius</i>				
Total length				
12	2	125.0	124–125	
13	6	132.7 \pm 7.04	120–143	6.5
Length of tail				
12	2	44.0	44	
13	6	48.7 \pm 2.29	46–54	5.8
Length of hindfoot				
12	2	15.0	15	
13	6	16.0 \pm 0.52	15–17	4.0
Length of ear				
12	2	13.0	13	
13	6	13.7 \pm 0.42	13–14	3.8
Weight				
12	1	19.0		
13	6	16.2 \pm 2.75	13–22	20.9
Greatest length of skull				
12	2	21.7	21.1–22.3	
13	5	20.4 \pm 0.88	21.3–23.9	4.5

Table 5.—Continued.

Sam- ple	N	Mean \pm 2 SE	Range	CV
Condylobasal length				
12	2	20.3	19.9–20.7	
13	6	21.0 \pm 0.76	20.1–22.5	4.5
Zygomatic breadth				
12	2	11.1	10.8–11.3	
13	6	11.8 \pm 0.38	11.2–12.4	4.0
Interorbital breadth				
12	2	3.7	3.7	
13	6	3.9 \pm 0.16	3.6–4.1	5.0
Rostral breadth				
12	1	4.1		
13	6	4.2 \pm 0.24	3.9–4.7	6.9
Oblique length of bulla				
12	2	4.7	4.5–4.9	
13	5	4.8 \pm 0.23	4.4–5.0	5.3
Greatest length of bulla				
12	2	7.3	6.9–7.6	
13	5	7.4 \pm 0.19	7.1–7.7	2.9
Length of maxillary toothrow				
12	2	3.7	3.6–3.8	
13	6	3.8 \pm 0.12	3.6–4.0	3.9
Breadth across upper molars				
12	2	5.0	5.0	
13	6	5.3 \pm 0.19	5.1–5.7	4.4
Length of anterior palatal foramen				
12	2	3.8	3.5–4.1	
13	6	4.2 \pm 0.18	4.0–4.6	5.3
Length of posterior palatal foramen				
12	2	0.5	0.4–0.5	
13	4	0.4 \pm 0.08	0.3–0.5	20.4
Length of diastema				
12	2	4.9	4.7–5.0	
13	6	5.3 \pm 0.35	4.8–5.9	8.0
Height of skull				
12	2	7.6	7.5–7.6	
13	6	8.2 \pm 0.18	8.0–8.5	2.7
Length of mandibular toothrow				
12	2	3.1	3.0–3.2	
13	6	3.4 \pm 0.12	3.2–3.6	4.5

The holotype of *S. jacksoni* is an individual that is a very old age category III or a young age category IV animal (Table 5, Sample 8). However, even if placed as an age category III individual, it still falls within the normal variation of cranial measurements of *S. caurinus*. Zygomatic breadth of the holotype appears to be relatively narrow even for an age III specimen.

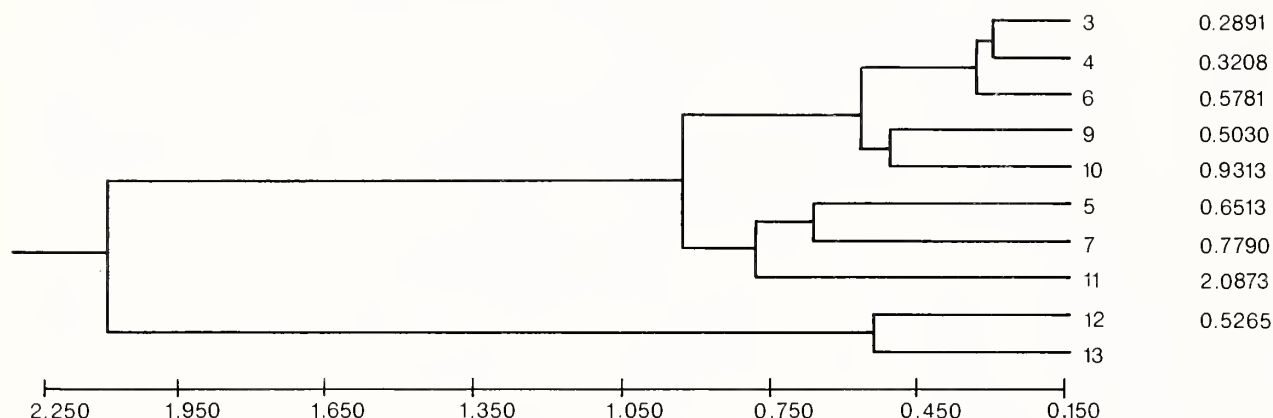


Fig. 3.—Distance phenogram of OTUs (see Fig. 2 and text for key to localities included in each OTU) of West African taxa of *Steatomys* computed from distance matrix based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). OTUs consist of geographic samples of combined sexes. The cophenetic correlation for the phenogram is 0.94.

Multivariate analysis.—Twelve cranial measurements of 10 geographic samples of age category III specimens of combined sexes were analyzed using the NT-SYS routines. Length of posterior palatal foramen and greatest length of skull were excluded from this analysis. Inclusion of greatest length of skull would have caused reduced geographic samples (such as deletion of sample 10) and sample sizes because of missing data.

A distance phenogram diagramming the relationship among 10 geographic samples (OTUs) of *Steatomys* is shown in Fig. 3. The cophenetic correlation coefficient for the phenogram is 0.946. The geographic samples fall into two major clusters. The upper group (OTUs 3, 4, 6, 9, 10, 5, 7, 11) represents medium- to large-sized individuals presently assigned to *S. caurinus*. The lower group represents small individuals from localities in Senegal (OTU 12) and Panisau, Nigeria (OTU 13) and corresponds to the presently recognized *S. cuppedius*.

The first three principal components computed from the matrix of correlation among 12 cranial characters for the same 10 geographic samples (OTUs) are shown in Fig. 4. The proportion of the total phenetic variation accounted for in the first three components is 95.3%. The amounts of variance assigned to each component are 86.9% for component I, 5.2% for component II, and 3.2% for component III. A factor matrix of character loadings among the 12 cranial characters of the principal component analysis is given in Table 6. From the factor analysis it can be seen that the first principal component is heavily influenced by general overall

cranial size. The second component is influenced most by length of mandibular toothrow, and the third by interorbital breadth. Examination of the three-dimensional plot (Fig. 4) reveals an expression of phenetic variation similar to that shown in the distance phenogram (Fig. 3); overall cranial size is expressed as progressively larger from left to right. OTUs 12 (Senegal) and 13 (Panisau, Nigeria) cluster on the left, and all other samples cluster in a fairly loose group on the right. Subgroupings within the right cluster of OTUs correspond with those found in the distance phenogram. These subgroupings will be discussed in detail in the systematic accounts that follow.

Taxonomic Conclusions

We interpret the univariate and multivariate analyses to indicate that in West Africa the genus *Steatomys* is represented by three species. Geographically, they are distributed as follows: *Steatomys caurinus* is known from Senegal, Ivory Coast, Upper Volta, Ghana (excluding Wenchi), Togo, Benin, and central Nigeria; *S. cuppedius* from Senegal, northern Nigeria, and south central Niger; and *S. jacksoni* from Wenchi, Ashanti District, Ghana. The latter species is known only from the holotype. *Steatomys cuppedius* is clearly the smallest of the three. *S. jacksoni* and *S. caurinus* are similar in size; the only appreciable difference between them is the size of the interparietal bone, with *S. jacksoni* having a significantly larger one. Little variation in size and shape of this bone is present in all of the

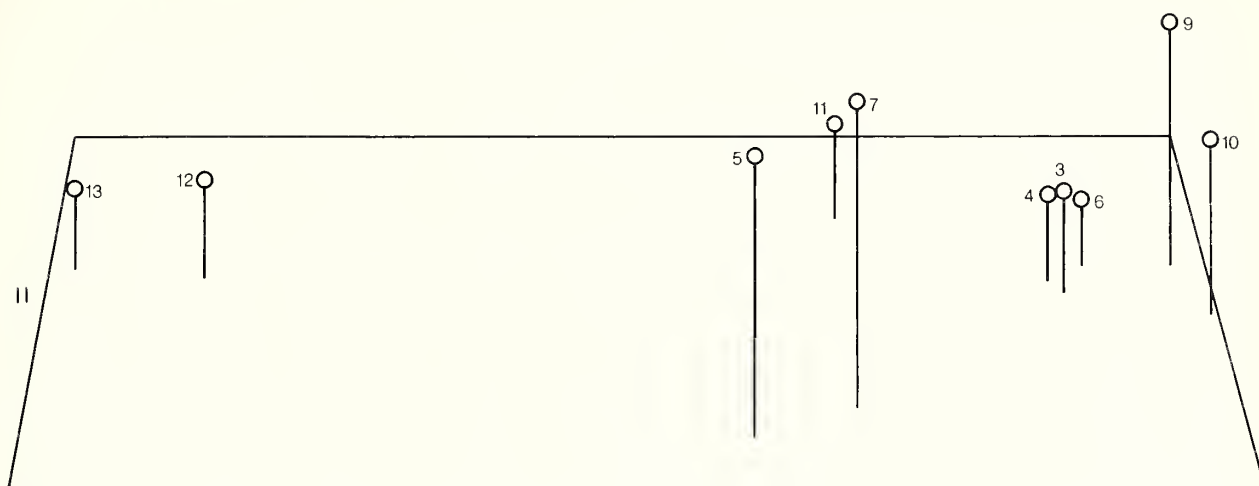


Fig. 4.—Three-dimensional projection of 10 OTUs of West African taxa of *Steatomys* on to the first three principal components based upon a matrix of correlation among 12 cranial measurements. OTUs consist of geographic samples of combined sexes. See Fig. 2 and text for key to localities included in each OTU. Component I accounts for 86.9% of the phenetic variation, component II for 5.2%, and component III for 3.2% for a combined expression of 95.3% of the total variation.

other material examined of the genus from West Africa. The possibility that the holotype of *S. jacksoni* might be an aberrant individual is recognized, but until additional specimens from the vicinity of the type locality of *S. jacksoni* are available for study, we prefer to retain this taxon as a valid species.

Hubert et al. (1973) reported *S. caurinus* from Senegal but presented no measurements. The genus

Steatomys, with no species given, has also been reported from owl pellets collected from Senegal (Heim de Balsac, 1965, 1967), but once again no measurements were given. The material upon which these reports were based has not been examined by us. We did not have available any *S. caurinus* from Senegal and feel this record should be reexamined to see if the material might be *S. cuppedius*.

SYSTEMATIC ACCOUNTS

Within the following accounts, species and subspecies, if appropriate, are listed in alphabetical order.

Steatomys caurinus Thomas, 1912

Geographic distribution of species.—Central Nigeria, southern Niger, northern Benin, Togo, western Ghana, Upper Volta, central to northern Ivory Coast, and Senegal (Fig. 2); most certainly more widespread and occurring in intervening areas.

Diagnosis.—Large, both externally and cranially, for genus in West Africa; pelage dark and individual hairs coarse; relatively small molars; interparietal bone short in length, usually less than 3.5 mm.

Comparisons.—*Steatomys caurinus* can be distinguished from *S. cuppedius* by a number of char-

acters. Comparisons of greatest length of skull, condylobasal length, greatest length of bulla, and length of diastema show no overlap in measurements of age category III specimens between these two species. These same four characters, and an additional eight measurements, indicate no overlap between age category IV specimens of the two species. These eight are total length, length of ear, weight, zygomatic breadth, rostral breadth, oblique length of bulla, width across upper molars, length of anterior palatal foramen, and height of skull.

Externally, *S. caurinus* can be separated from *S. cuppedius* by dark color of pelage and coarse texture of the hairs as opposed to the pale color of pelage and silky texture of the hairs in the latter species.

From *S. jacksoni*, *S. caurinus* differs little in ex-

Table 6.—Factor matrix of character loading of the first three principal components among 12 characters of West African taxa of *Steatomys* (left) and of *Steatomys caurinus* (right).

Character	<i>Steatomys</i> (three species)			<i>Steatomys caurinus</i>		
	Component I	Component II	Component III	Component I	Component II	Component III
Condylobasal length	0.996	0.007	−0.021	0.983	−0.076	0.036
Zygomatic breadth	0.958	0.089	−0.053	0.972	0.044	0.032
Interorbital breadth	0.849	−0.027	0.496	0.547	−0.133	−0.619
Rostral breadth	0.980	0.020	−0.089	0.941	0.046	0.146
Oblique length of bulla	0.874	−0.389	−0.244	0.283	0.810	0.424
Greatest length of bulla	0.985	0.043	−0.014	0.921	−0.236	−0.058
Length of maxillary toothrow	0.879	0.248	−0.092	0.568	−0.463	0.511
Breadth across upper molars	0.952	−0.242	0.051	0.692	0.497	−0.315
Length of anterior palatal foramen	0.921	0.154	0.157	0.804	−0.254	−0.315
Length of diastema	0.969	−0.191	−0.093	0.808	0.486	0.233
Height of skull	0.961	−0.169	0.063	0.752	0.289	−0.197
Length of mandibular toothrow	0.845	0.503	−0.139	0.719	−0.608	0.301

ternal or cranial dimensions nor, as far as we can tell, in color of pelage. The single character for distinguishing these two species is the longer length of interparietal bone in *S. jacksoni* than in *S. caurinus*; a length of 4.5 mm in the former versus less than 3.5 mm, in fact except for a few individuals, less than 3.0 mm in the latter.

Geographic Variation

Univariate analysis.—In examining geographic variation in *S. caurinus*, five external and 14 cranial measurements of age category III individuals were examined and the following results were found (Table 4). The specimens of the combined geographic sample from Yama and Sienso (OTU 11) of north-western Ivory Coast are clearly smaller than are those of all of the other geographic samples tested in nine of the 19 characters examined. These nine characters are total length, greatest length of skull, condylobasal length, zygomatic breadth, rostral breadth, oblique length of bulla, width across upper molars, length of diastema, and height of skull.

The geographic sample from Tyenko (OTU 9), which is less than 100 mi south of OTU 11, and that from Diali (OTU 10), which is from still farther south and east in Ivory Coast than OTU 9, are both clearly larger than are the remaining geographic samples of *S. caurinus* examined in total length, length of tail, greatest length of skull, condylobasal length, length of anterior palatal foramen, and height of skull. OTUs 9 and 10 are even more strikingly large when compared with OTU 11, the geographic sample exhibiting the smallest dimensions

for the species. Three specimens were available for study from Diali (OTU 10); two of these specimens were large for the species. Diali and also the type locality of *S. jacksoni* (Wenchi, Ghana) are situated on the interface of the High forest and Invasive woodland in West Africa. The holotype of *S. jacksoni* and the two large specimens from Diali are comparable in size, except for length of interparietal.

There is no indication of a trend in variation in hindfoot length although OTU 3 (Pirisi, Ghana) and OTU 4 (Gudi, Nigeria) tend to have relatively long hindfeet when compared to the other geographic samples. The same discordant pattern is apparent in the variation in the length of the ear, although there is no clear grouping of geographic areas into different size groups, OTU 11 displayed relatively long ears. In both instances, this discordance could be an artifact of different techniques used by preparators of skins. The cranial characters of interorbital breadth, length of maxillary toothrow, length of posterior palatal foramen, and length of mandibular toothrow show little geographic variation.

Considering the vast distances involved (about 1200 km), the geographic samples from OTU 3 in Ghana, OTU 6 in Upper Volta, and OTU 4 in Nigeria show little geographic variation in the characters tested.

Multivariate analysis.—Twelve cranial measurements of eight geographic samples of age category III specimens of combined sexes were analyzed using the NT-SYS routines. Again the length of posterior palatal foramen and greatest length of skull were excluded from the analysis. A distance phe-

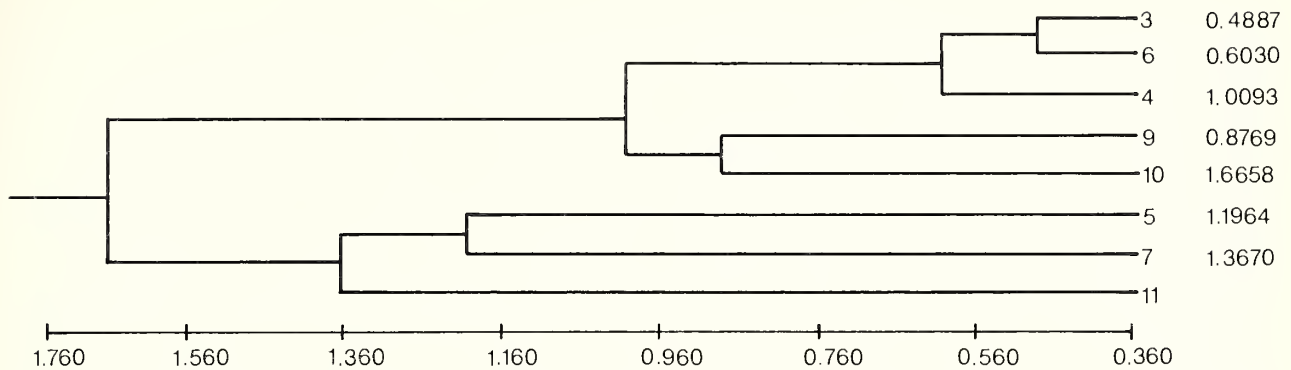


Fig. 5.—Distance phenogram of OTUs (see Fig. 2 and text for key to localities included in each OTU) of *Steatomys caurinus* computed from distance matrix based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). OTUs consist of geographic samples of combined sexes. The cophenetic correlation for the phenogram is 0.87.

nogram showing the relationship among eight geographic samples of *Steatomys caurinus* is illustrated in Fig. 5. The cophenetic correlation coefficient for the phenogram is 0.87. The OTUs separate into two major groups. The upper one (OTUs 3, 6, 4, 9, and 10) includes individuals of medium to large cranial dimensions. This group further clusters into two subgroups—OTUs 9 (Tyenko) and 10 (Diali) from the Ivory Coast are included in one subgroup, and OTUs 3 (Pirisi, Ghana), 4 (Gudi, Nigeria), and 6 (Cella, Upper Volta) in a second subgroup. Of these two subgroups, the former subgroup consists of the larger sized individuals of the two subgroups. Although OTUs 9 and 10 are paired together on the phenogram, they are well separated by phenetic distance. The lower major group consists of three OTUs paired together but well separated by phenetic distance; OTUs 5 and 7 from Upper Volta, and OTU 11 from Yama and Sienso, Ivory Coast.

The first three principal components computed from the matrix of correlation among 12 cranial characters for eight geographic samples (OTUs) of *Steatomys caurinus* are presented in Fig. 6. The amount of phenetic variation represented in each of the first three components is 60.1% for component I, 16.3% for component II, and 10.2% for component III, for a total expression of 86.6% of the total phenetic variation. A factor matrix of character loadings from correlation among the 12 cranial characters is given in Table 6. From Table 6, it can be seen that the first, and by far the most important, component is heavily influenced by general cranial size; especially those measurements expressing length of skull, breadth of zygoma and rostrum, and greatest length of bulla. Interorbital breadth,

oblique length of bulla, and length of maxillary tooththrow show relatively low values for component I. Component II is influenced positively by oblique length of bulla and negatively by length of mandibular tooththrow, whereas component III has a high positive value for length of maxillary tooththrow and a high negative value for interorbital breadth.

Examination of the three-dimensional plot of the principal components (Fig. 6) reveals a pattern of variation in accordance with that shown in the distance phenogram (Fig. 5). OTUs 5, 7, and 11 form one main group on the left, with each OTU distantly separated from each other. The other major grouping, consisting of OTUs 3, 4, 6, 9, and 10 forms two subclusters with OTUs 3, 4, and 6 constituting the one and OTUs 9 and 10 the other.

This projection plot indicates that OTU 11 consists of individuals with small overall cranial size, especially with short and narrow skulls (Table 6). Although the overall length of bulla, including mastoid portion, is long, the audital portion, as expressed in component II, is shortened. Component II also indicates a relatively long mandibular tooththrow compared to OTUs 5 and 7. Interorbital breadth of individuals of OTU 11 is narrow as shown by the negative influence of this character on component III. Component III indicates a long maxillary tooththrow for OTU 11.

OTUs 5 and 7 from Upper Volta are small in overall size. Both are well separated from OTU 11 in components II and III by the characters mentioned above. In spite of having generally short and narrow skulls, their scores for component III indicate a relatively broad interorbital region and short maxillary tooththrow, the latter corresponding with

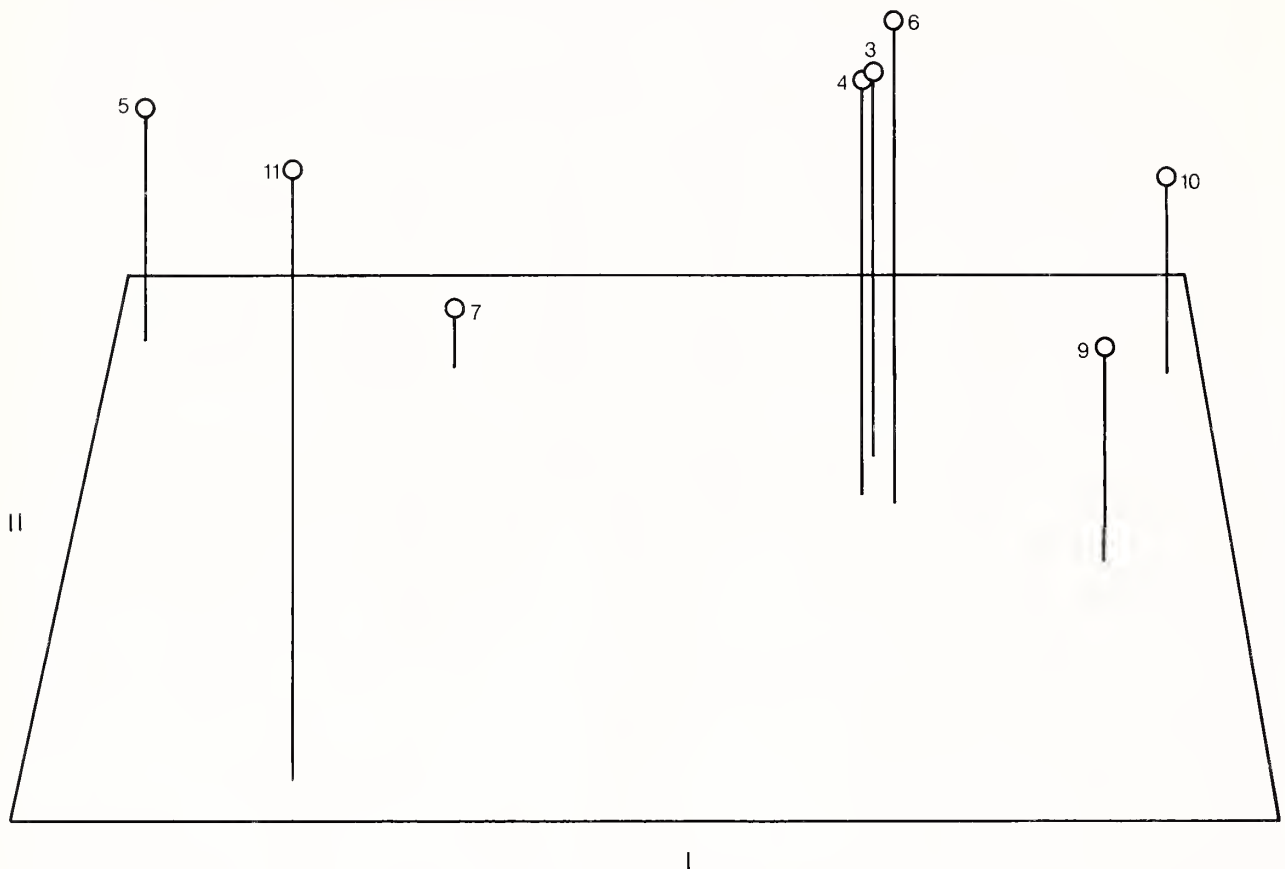


Fig. 6.—Three-dimensional projection of eight samples of *Steatomys caurinus* on to the first three principal components based upon a matrix of correlation among 12 cranial measurements. OTUs consist of geographic samples of combined sexes. See Fig. 2 and text for key to localities included in each OTU. Component I accounts for 60.1% of the phenetic variation, component II for 16.3%, and component III for 10.2% for a combined expression of 86.6% of the total variation.

their short mandibular tooththrow as expressed on component II.

The other geographic samples from Ivory Coast (OTUs 9 and 10), represented by a maximum of five and three specimens, respectively, contain large individuals. These OTUs are essentially equal in skull dimensions as expressed in components I and III, but separate somewhat based on component II—an expression of length of auditory bulla and, inversely, length of mandibular tooththrow.

The OTUs 3, 4, and 6 are all represented by large sample sizes (minimum of 18 specimens), and are morphologically identical even though 1,200 km separate OTU 3 from 4. Other than slight differences in overall size of skull, and slightly narrower interorbital region and longer maxillary tooththrow, OTUs 3, 4, and 6 differ little from OTUs 9 and 10.

Taxonomic Conclusions

Based on our assessment of geographic variation, we have separated *S. caurinus* into two taxonomically recognizable populations. The smallest individuals in the species belong to the population from Yama and Sienso in northwestern Ivory Coast and are herein described as a new subspecies. A second subspecies, *S. caurinus caurinus* Thomas, 1912, represented by mice of medium to large size, is known from Tyenko and Diali, Ivory Coast, Upper Volta, Ghana, Togo, Benin, and Nigeria. OTUs 2 and 6 from Upper Volta represent relatively small individuals, but, considering the small sample sizes and geographic distribution of the OTUs involved, is retained in *S. c. caurinus*. Further samples are required from within the areas between the Yama and Sienso (Ivory Coast) localities and Ghana

(OTU 2) and Upper Volta (OTUs 5 and 7) populations in order to determine the distribution of the new subspecies and its relationships to the populations at the latter localities. Also the taxonomic and distributional status of the individuals of large size from Tyenko (OTU 9) and Diali (OTU 10), Ivory Coast, is deserving of additional study.

***Steatomys caurinus caurinus* Thomas, 1912**

1912. *Steatomys caurinus* Thomas, Ann. Mag. Nat. Hist., ser. 9, 9:271, February.

1977. *Steatomys pratensis caurinus*, Coetzee, in Meester and Setzer (eds.), The mammals of Africa . . . , Smithsonian Inst. Press, 6-8:1-4.

Holotype.—Young adult female (age category III), skin and skull BMNH 12.1.16.24, from Panyam, 4,000 ft, Nigeria; obtained 13 July 1911 by Rev. G. T. Fox, original number 47. Skin in good condition; skull with left occipital region broken, both bullae separated from skull but repaired with glue, left zygoma broken.

Measurements of holotype.—Total length, 164; length of tail, 54; length of hindfoot, 19; length of ear, 19; greatest length of skull, 27.3; interorbital breadth, 3.9; rostral breadth, 4.8; length of maxillary tooththrow, 4.0; breadth across upper molars, 6.1; length of anterior palatal foramen, 5.0; length of diastema, 7.2; length of mandibular tooththrow, 3.4.

Distribution.—Known from Ivory Coast (Tyenko and Diali), Upper Volta, western and northern Ghana, northern Togo and Benin, and central Nigeria. Literature records indicate its occurrence in Senegal as well.

Comparisons.—For comparisons of *Steatomys caurinus caurinus* with other taxa from West Africa, see each of the following accounts.

Remarks.—The subspecies *S. c. caurinus* consists of individuals of medium to large size for the species and seems to occur over an extensive geographic area from at least Ivory Coast east to Nigeria, although originally known only from Nigeria (Thomas, 1912a, 1912b). Within this area, specimens are generally uniform in size and in shape of skull. In the Ivory Coast, specimens of two sizes have been reported by Heim de Balsac (1967). For additional comments on this material, see the following account.

Steatomys caurinus was reported from Bandia, Senegal, by Hubert et al. (1973). Heim de Balsac (1967:219) reported a large and a small *Steatomys*

from M'Bour, Senegal. We are accepting both locality records as *S. caurinus* at this time but are unable to assign with certainty this material to subspecies. Because the relationship of the Senegalese specimens could well be to the populations of the Sudan Woodland of Upper Volta, we are listing the literature records under the nominate subspecies. Based on these published reports, it appears that the only locality of sympatry between *S. caurinus* and *S. cuppedius* in West Africa would be M'Bour, Senegal.

Specimens examined (196).—BENIN: Kouande, 1 (USNM). GHANA: Bawku, 1,400 ft, 1 (BMNH); Bangwon, 5 (USNM); Pirisi, 43 (USNM); Sakpa, 1 (USNM). IVORY COAST: Bouna, 1 (USNM); Diali, 14 (USNM); Tyenko, 12 (USNM). NIGERIA: 3 mi E Gudi, 52 (USNM); Panyam, 4,000 ft, 11 (BMNH). TOGO: Dapango, 1 (USNM); 1 km N Cella, 48 (USNM); Dio, 1 (USNM); Fo, 1 (USNM); 36 mi SE Nayoure, 1 (USNM).

Additional records.—IVORY COAST: Lamto (Bellier, 1967; Heim de Balsac and Bellier, 1967:159; Bellier and Gatun, 1968:708; Heim de Balsac, 1967:215-219); Bouake (Heim de Balsac, 1967; Heim de Balsac and Bellier, 1967:159; Bellier and Gatun, 1968:708). SENEGAL: Bandia (Hubert et al., 1973:81), M'Bour (Heim de Balsac, 1967:219).

***Steatomys caurinus roseveari*, new subspecies**

Holotype.—Adult male, skin and skull, USNM 467496, from Yama, Ivory Coast; obtained on 22 March 1969 by L. W. Robbins, original number 1106. Skin in good condition, missing left front foot; skull in good condition, nasals damaged.

Measurements of holotype.—Total length, 156; length of tail, 47; length of hindfoot, 18; length of ear, 17; weight, 42 g; condylobasal length, 25.3; zygomatic breadth, 13.0; interorbital breadth, 4.1; rostral breadth, 5.0; oblique length of bulla, 5.5; greatest length of bulla, 9.1; length of maxillary tooththrow, 4.2; breadth across upper molars, 5.8; length of anterior palatal foramen, 5.6; length of posterior palatal foramen, 0.4; height of skull, 9.9; and length of mandibular tooththrow, 3.2. Additional measurements are listed in Tables 3, 4, and 5.

Distribution.—At present known only from Sienso and Yama in northwestern Ivory Coast.

Comparisons.—*Steatomys caurinus roseveari* can be distinguished from *S. c. caurinus* by its smaller size, especially cranial dimensions. Most characteristic of this new subspecies are short and narrow skulls with relatively narrow interorbital region and long maxillary and mandibular tooththrows. From *S. jacksoni* and *S. cuppedius*, *S. c. roseveari* can be separated as for the species.

Remarks.—Heim de Balsac (1967) considered the

taxonomic status of *Steatomys* in the Ivory Coast but failed to put specific epithets on his specimens. Heim de Balsac (1967:216–220) reported large and small specimens from Bouake and Lamto. Without having examined these specimens, we are unable to make a definitive judgment. It is possible these differences are attributable to nongeographic variation such as age (certainly at least specimens A and D in figure 14 of Heim de Balsac, 1967, are young animals) or there might be two distinct taxa represented. *S. caurinus roseveari* is smaller than the nominate subspecies. The small form reported by Heim de Balsac (1967) might represent this new subspecies. If this were true, and it was sympatric with *S. caurinus caurinus*, then each must be recognized as distinct species. In the geographic sample from Tyenko (OTU 9) or Diali (OTU 10) we could not find any evidence of intergradation or of two distinct morphotypes being present. For now we consider these small individuals from Tyenko and Diali to be a subspecies of *S. caurinus*.

Etymology.—This new subspecies is named for D. R. Rosevear who has contributed much, both in the field and in print, to the study of the mammals of West Africa. His monumental written contributions will serve for many years as a primary reference for anyone interested in bats, rodents, or carnivores of this fascinating region of Africa. For his abundant contributions after his retirement and return to England from Nigeria, all who study small mammals in West Africa owe him a large amount of gratitude.

Specimens examined (75).—IVORY COAST: Sienso, 6 (USNM); Yama, 69 (USNM).

***Steatomys cuppedius* Thomas and Hinton, 1920**

Geographic distribution of species.—Known from northern Nigeria, southern Niger, and Senegal.

Diagnosis.—Small, both externally and cranially, for the genus in West Africa; condylobasal length of skull less than 20.7 mm; length of maxillary toothrow usually less than 4.0 mm; pelage pale in color, with individual hairs soft.

Comparisons.—From all other species of *Steatomys* occurring in West Africa, *S. cuppedius* can be separated by its small size, both externally and cranially. Skulls of *S. cuppedius* are less than 20.7 mm in condylobasal length in age category III individuals.

Geographic Variation

Univariate analysis.—Five external and 14 cranial measurements of age category III individuals of *Steatomys cuppedius* from Senegal and Nigeria

were examined for geographic variation. The geographic sample from Senegal is larger in size than is the one from Nigeria (Table 4). Of age category III individuals, four measurements (total length, weight, greatest length of skull, and oblique length of bulla) of the populations from Senegal were significantly larger than those from Nigeria. Nine other measurements averaged larger and four averaged smaller, whereas two were equal in size (Table 4). Only small samples of age category IV were available for analysis of geographic variation (Table 5). A trend similar to that found in age category III is not indicated in such small samples.

Taxonomic Conclusions

Only three geographic samples of *S. cuppedius* were examined—a single individual from Niger and two geographic samples of sizeable proportions from Senegal and Nigeria. Considering the distance of approximately 2,500 km between the geographic samples from Senegal and Nigeria, the geographic variation present is not striking. Taxonomic separation of these localities is not warranted; we consider *Steatomys cuppedius* to be a monotypic species.

***Steatomys cuppedius* Thomas and Hinton, 1920**

1920. *Steatomys cuppedius* Thomas and Hinton, Novit. Zool., 27:318, 15 June.

1977. *Steatomys parvus cuppedius*, Coetzee, in Meester and Setzer (eds.), *The mammals of Africa . . .*, Smithsonian Inst. Press, 6:8:1–4.

Holotype.—Adult female (age category IV), skin and skull, BMNH 21.2.11.85, from Farniso (=Panisau), near Kano, 1,700 ft, Nigeria; obtained 29 December 1919 by A. Buchanan, original number 70. Skin in good condition; skull in fair condition, left zygoma broken.

Measurements of holotype.—Total length, 124; length of tail, 43; length of hindfoot, 14; length of ear, 14; greatest length of skull, 21.3; condylobasal length, 20.4; interorbital breadth, 3.6; rostral breadth, 4.2; greatest length of bulla, 7.7; breadth across upper molars, 5.2; length of anterior palatal foramen, 8.8; length of diastema, 5.2; height of skull, 8.0; length of mandibular toothrow, 3.0.

Distribution.—This species is known from central Nigeria, Niger, and Senegal.

Comparisons.—See comparisons for species.

Remarks.—Originally described from material from northern Nigeria (Thomas and Hinton, 1920, 1921), *Steatomys cuppedius* has been uncommon in

collections of rodents from West Africa. Thomas (1925:194) reported a single specimen from Gangara, Niger, a locality across the Nigerian border to the northeast from the type locality. Although large numbers of *Steatomys* from Upper Volta were available, none proved to be *S. cuppedius*. If the latter occurs in Upper Volta, it will probably be found in the extreme north and have a distribution similar to *Gerbillus nigeriae*, as it seems to have in Nigeria.

There seems to be some doubt as to the identity of the skulls reported from owl pellets by Heim de Balsac (1965). Later, Heim de Balsac and Bellier (1967) indicate that the material from "nord de Saint-Louis du Senegal" and "au voisinage de M'Bour" was smaller than the material obtained in Ivory Coast. If this is true, it is likely this Senegalese material belongs to *S. cuppedius* although we are unable to identify it with certainty. We have included these records under the additional records of this species.

Specimens examined (113).—NIGER: Gangara, 1,400 ft, 1 (BMNH). NIGERIA: Farniso, near Kano, 1,700 ft, 6 (BMNH); Panisau, 55 (USNM). SENEGAL: 17 km NE Kiourbel, 1 (USNM); 15 km N Karrfine, 16 (USNM); 6 km E Kaolack, 7 (USNM); Koungheul, 27 (USNM).

Additional records.—SENEGAL: north of St. Louis, (Heim de Balsac, 1967:219; Heim de Balsac and Bellier, 1967:159); M'Bour (Heim de Balsac and Bellier, 1967:159).

Steatomys jacksoni Hayman, 1936

Geographic distribution of species.—Known only from the type locality, Wenchi, Ashanti [district], Ghana.

Diagnosis.—Size large, both externally and cranially, for genus in West Africa; skull long and relatively narrow; interparietal bone long, 4.5 mm in length.

Comparisons.—For comparisons with *S. cuppedius* and *S. caurinus*, see accounts of that species and for additional comments, see section "Relationships of Species."

Steatomys jacksoni Hayman, 1936

1936. *Steatomys jacksoni* Hayman, Proc. Zool. Soc. London, for 1935, pp. 930, 10 January.

1977. *Steatomys pratensis jacksoni*, Coetzee, in Meester and Setzer (eds.), The mammals of Africa . . . , Smithsonian Inst. Press, 6:8:1-4.

Holotype.—Young adult male (young age category IV), skin and skull BMNH 35.1.30.157, from Wenchi, Ashanti, Ghana; obtained 18 January 1934 by W. P. Lowe, original number 104. Skin and skull in good condition.

Measurements of holotype.—Total length, 170; length of tail, 50; length of hindfoot, 18; length of ear, 18; greatest length of skull, 28.5; condylobasal length, 27.1; zygomatic breadth, 12.9; interorbital breadth, 4.0; rostral breadth, 5.3; oblique length of bulla, 5.8; greatest length of bulla, 9.6; length of maxillary tooththrow, 4.0; breadth across upper molars, 6.1; length of anterior palatal foramen, 5.7; length of diastema, 7.2; height of skull, 10.0; length of mandibular tooththrow, 3.7.

Distribution.—Same as given above.

Comparisons.—See comparisons given above.

Remarks.—We prefer to retain this taxon as a valid species based solely on the size and shape of the interparietal bone. Additional material from the type locality is required before a critical evaluation of variation in the interparietal bone can be made.

Specimens examined (1).—GHANA: Wenchi, Ashanti, 1 (BMNH).

ACKNOWLEDGMENTS

We are indebted to the following institutions and curators who made available West African *Steatomys* specimens for study. Abbreviations preceding the names of institutions are used in the accounts above to identify the source of specimens.

BMNH—British Museum (Natural History), London (I. Bishop).

USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, D. C. (Henry W. Setzer).

We are grateful to Hugh H. Genoways for helping us in many ways, besides critically reading the manuscript; Flora Gibson for

typing early drafts of it, and Teresa Bona for typing and critically editing later drafts; Terry L. Yates for performing the NT-SYS computations on the Texas Tech University computers; Judy Schlitter for keypunching; Margaret Popovich for proofreading tables; Nancy Perkins for preparing the figures; and John Sutton for help with computer-facilitated statistical analyses.

This research was performed while the senior author visited the Section of Mammals as a Resident Museum Specialist in the International Visitor Program of Carnegie Museum of Natural History.

GAZETTEER

Names of geographic features listed below are those used in the text. The primary sources for spellings and coordinates of localities were the individual specimen tags and the gazetteers of the United States Board on Geographic Names (prepared by the Office of Geography, Department of Interior).

BENIN:	Kouande	10 20 N, 01 41 E
GHANA:	Bangwon	10 58 N, 02 41 W
	Bawku	11 05 N, 00 11 W
	Pirisi	10 07 N, 02 27 W
	Sakpa	08 52 N, 02 21 W
	Wenchi	07 45 N, 02 02 W
IVORY COAST:	Bouake	07 41 N, 05 02 W
	Bouna	09 16 N, 03 00 W
	Diali	07 03 N, 05 37 W
	Katiola	08 08 N, 05 06 W
	Lamto	06 12 N, 04 58 W
	Ouango Fitini	09 34 N, 04 03 W
	Sienso	09 25 N, 07 31 W
	Tyenko	08 14 N, 07 24 W
	Yama	09 36 N, 06 19 W

NIGER:	Gangara	ca. 14 00 N, 09 00 E
NIGERIA:	Farniso [=Panisau]	
	Gudi	08 54 N, 08 17 E
	Panisau (Panisa)	11 43 N, 07 32 E
SENEGAL:	Bandia	14 37 N, 17 02 W
	Diourbel	14 40 N, 16 15 W
	Kaffrine	14 06 N, 15 33 W
	Kaolack	14 06 N, 16 33 W
	Koungheul	13 59 N, 14 48 W
	M'Bour	14 24 N, 16 58 W
	St. Louis	16 02 N, 16 30 W
TOGO:	Dapango	10 52 N, 00 13 E
	Wulehe	08 40 N, 00 00
UPPER VOLTA:	Barga	13 51 N, 02 12 W
	Cella	11 38 N, 00 22 W
	Dio	13 20 N, 02 38 W
	Fo	11 53 N, 04 31 W
	Nayoure	12 15 N, 00 16 E

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A CRITICAL EXAMINATION OF ALLEGED SIBLING SPECIES IN THE LESSER THREE-TOED JERBOAS (SUBGENUS *JACULUS*) OF THE NORTH AFRICAN AND ARABIAN DESERTS

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ABSTRACT

Alleged sibling speciation in the lesser three-toed jerboas is considered. Variation in supposed diagnostic characters is ex-

amined. *Jaculus deserti* Loche, 1867, is shown to be a junior synonym of *J. jaculus* Linnaeus, 1758.

INTRODUCTION

Ellerman and Morrison-Scott (1951) in their comprehensive review of Palaearctic mammals recognized only three species of this subgenus, namely *Jaculus jaculus* Linnaeus, 1758, *Jaculus blanfordi* Murray, 1884, and *Jaculus orientalis* Erxleben, 1777. The validity of these three taxa is not in doubt, but recently the suggestion has been made (Ranck, 1968) that two sibling species exist within the populations of the lesser three-toed jerboa, *Jaculus jaculus*, occurring in northern Africa and the Arabian Peninsula. For one of these sibling species Ranck (1968) has employed an old taxon, *Jaculus deserti*, based on *Dipus deserti* Loche, 1867.

Ranck (1968) keyed these two species as follows:

Dorsal color dark; two foramina on angular process of mandible; sole of hind foot and metatarsal area suffused with brownish hairs *J. deserti*

Dorsal color pale; a single foramen on angular process of mandible; sole of hind foot and metatarsal area white or buff and lacking suffusion of brownish hairs *J. jaculus*

Ranck (1968) gave the range of his *J. deserti* as Arabia, Iraq, Israel, Sinai, Egypt, Libya, and Algeria and referred the following taxa as subspecies of it: *J. deserti deserti* Loche, 1867; *J. deserti vastus* Ranck, 1968; *J. deserti rarus* Ranck, 1968; *J. deserti fuscipes* Ranck, 1968; *J. deserti favillus* Setzer, 1955; *J. deserti schluteri* Nehring, 1901; *J. deserti vocator* Thomas, 1921; and *J. deserti loftusi* Blanford, 1875.

For *Jaculus jaculus* Ranck (1968) gave the general range as Iraq, Syria, Lebanon, Israel, Jordan,

Saudi Arabia, and North Africa south through the Sahara including Sudan, Chad, Niger, Mauritania, and Spanish Sahara. To this species Ranck referred the following taxa: *Jaculus jaculus jaculus* Linnaeus, 1758; *J. jaculus arenaceus* Ranck, 1968; *J. jaculus collinsi* Ranck, 1968; *J. jaculus cufrensis* Ranck, 1968; *J. jaculus tripolitanicus* Ranck, 1968; *J. jaculus whitchurchi* Ranck, 1968; *J. jaculus sefrius* Thomas and Hinton, 1921; *J. jaculus centralis* Thomas and Hinton, 1921; *J. jaculus butleri* Thomas, 1922. Other subspecies not specifically allocated by Ranck include *J. jaculus airensis* Thomas and Hinton, 1921; *J. jaculus favonicus* Thomas, 1913; *J. jaculus gordonii* Thomas, 1903; and *J. jaculus vulturinus* Thomas 1913.

Harrison (1972), reviewing the material of *Jaculus* from the Arabian Peninsula, has already thrown doubt on the validity of these "sibling species," stating "I am quite unable to distinguish two small species of *Jaculus* in the extensive Arabian material examined . . . individual variation in both coloration of the soles and size and number of the angular foramina is so extensive and random in the Arabian jerboas that the definition of two species on this basis appears quite impossible."

As a preliminary part of an extended investigation of geographical variation in *Jaculus*, it appeared necessary to make a critical examination of Ranck's sibling species criteria in North African as well as in the Arabian populations, in order to evaluate the problem more fully and prevent further systematic confusion. That is the purpose of the present study, which is not intended in any other way as a revision of the numerous geographical forms listed above. Such a revision must clearly await far more detailed and extensive research.

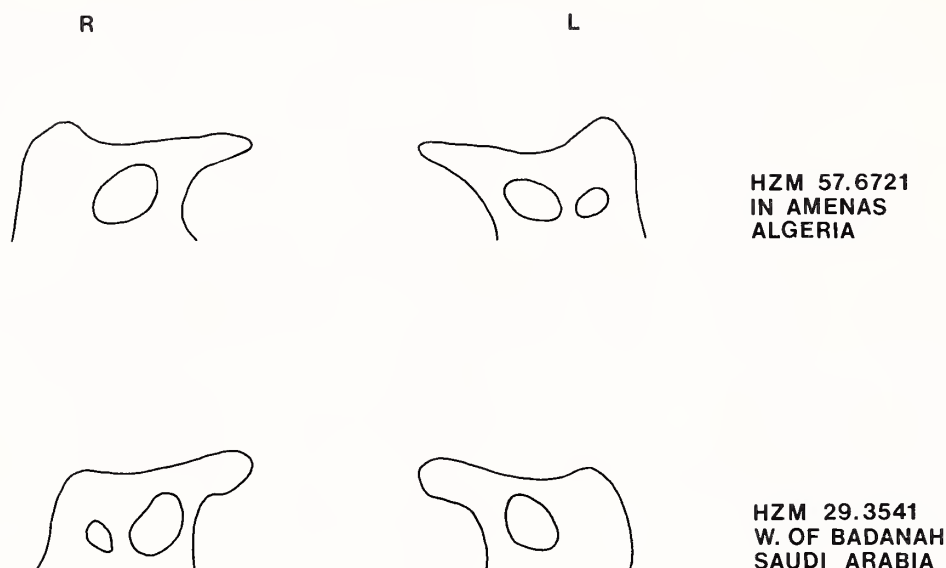


Fig. 1.—Examples of the angular processes of two specimens of *Jaculus jaculus* from Algeria and Saudi Arabia showing variation in angular foramina. Angular foramina scores are 1 - 2 above and 2 - 1 below. Abbreviations are R (right) and L (left); numbers are registry numbers for specimens in the Harrison Zoological Museum (HZM).

METHODS

Coloration

Of the characters employed by Ranck to separate *J. deserti* and *J. jaculus*, both dorsal coloration and sole coloration are necessarily somewhat subjective, but have been found susceptible to the method of scoring listed below, in each specimen examined:

Dorsal coloration

1. Pallid sandy
2. Grayish sandy
3. Brownish sandy

Paler
↓
Darker

Sole coloration

1. White
2. Buff
3. Brown

Paler
↓
Darker

A major source of confusion has been found to occur in the case of sole coloration in *Jaculus*, namely discoloration of the sole and digital brushes by the substrate. A most striking example of this was seen in a series of skins from In Amenas, Algeria, in which the soles and digital brushes are bright orange—until washed with water, when the orange discoloration disappears, leaving a white condition. With experience it is usually possible to distinguish discoloration from true pigmentation and washing is seldom required.

Angular Foramina

Fortunately, the angular foramina are easily evaluated and can be counted and recorded with stereomicroscopic drawings. Unfortunately, the angular process is delicate and hence often broken in preparation. It is pertinent to observe here that the angular foramina represent unossified areas in bone, which are occupied by membrane in life, a fact which no doubt accounts for their great variability, both in size and number.

These criteria have been recorded for each specimen examined and the results are summarized below in tabular form with all Arabian material and all North African material arranged in two separate groups. In these tables the scores for each specimen are arranged with dorsal coloration, sole coloration, and foramen counts for the right and left mandible in series from left to right, thus a score of 2:2:2-2 would indicate an animal with intermediate coloration of the dorsum and soles and two angular foramina on each side. The results are simply expressed as the number of individuals from each group showing each numerical score (where a mandibular foramen is broken or absent it is scored as x). Only those specimens able to provide a combination of dorsal and sole coloration with one or both angular foramen counts are included in this study; skins without skulls and skulls without skins are excluded. Each score is listed as being compatible (COM), incompatible (NC), or intermediate (INT).

RESULTS AND DISCUSSION

It is clear that if Ranck's hypothesis of two sibling species is correct, based on the characters given in his key, then both in African and Arabian populations two groups of scores ought to predominate in these results:

3 : 3 : 2 - 2
3 : 2 : 2 - 2
2 : 3 : 2 - 2

indicating the *deserti* species with dark or darkish dorsum and soles and two angular foramina. On the other hand, the following scores:

1 : 1 : 1 - 1
2 : 1 : 1 - 1
1 : 2 : 1 - 1

would indicate the *jaculus* species with pallid or palish dorsum and soles but one angular foramen.

On the other hand, scores including angular foramen counts of 2 - 1 or 1 - 2 ought not to occur at all, indicating both species foramen count in one individual (Fig. 1), and scores of

1 : 1 : 2 - 2
3 : 3 : 1 - 1

similarly should not occur at all, whereas the occurrence of many intermediate scores must cast further doubt on the validity of the hypothesis.

In both African and Arabian jerboas, scores for the angular foramina of 1 - 2 and 2 - 1 occur with such frequency (Table 1, Fig. 1) that on this consideration alone the sibling species hypothesis as advanced by Ranck simply cannot be upheld. Furthermore, the predicted scores for the two species do not predominate; other incompatible scores also occur at an unacceptable high incidence and intermediate scores form the highest percentage in both populations. The number of individuals assessed and percentage occurrences of compatible, incompatible, and intermediate scores are given in Table 2.

Table 2.—Summary of compatibility results for *Jaculus* from Table 1.

Compatibility	Arabia		Africa	
	Number	Percentage	Number	Percentage
Compatible	13	19	31	31
Incompatible	10	15	15	15
Intermediate	44	66	54	54
Total	67		100	

Table 1.—Scores obtained in this study for dorsal coloration, sole coloration, and angular foramina counts of *Jaculus*. Number of individuals with each score is indicated for each continent. COM = compatible, NC = not compatible, and INT = intermediate scores for Ranck's decision.

Compatibility	Score	Arabian Peninsula	Africa
COM	1:1:1 - 1	4	2
COM	1:1:X - 1	2	2
COM	1:1:1 - X	0	2
NC	1:1:1 - 2	2	0
NC	1:1:2 - 2	1	0
NC	1:1:2 - X	1	1
NC	1:1:X - 2	1	2
COM	1:2:1 - 1	1	19
COM	1:2:X - 1	0	4
COM	1:2:1 - X	0	1
NC	1:2:1 - 2	0	4
NC	1:2:2 - 1	0	3
INT	1:2:2 - 2	4	16
INT	1:2:2 - X	2	6
INT	1:2:X - 2	3	5
INT	1:2:2 - 3	0	3
INT	1:2:3 - 3	0	1
INT	1:2:2 - X	0	2
INT	1:3:2 - 2	0	2
INT	1:3:2 - X	1	2
NC	1:3:1 - X	1	0
INT	2:2:1 - 1	5	4
INT	2:2:X - 0	1	0
INT	2:2:X - 1	3	3
INT	2:2:1 - X	3	0
NC	2:2:1 - 2	1	0
NC	2:2:1 - 3	0	2
INT	2:2:2 - 2	8	5
INT	2:2:2 - X	5	0
INT	2:2:X - 2	5	4
NC	2:2:2 - 1	2	2
INT	2:2:3 - 2	1	1
INT	2:1:2 - 2	2	0
INT	2:1:2 - X	1	0
COM	2:3:2 - 2	2	0
COM	2:3:2 - X	2	0
COM	2:3:X - 2	2	0
NC	2:3:X - 1	1	0
COM	3:3:X - 2	0	1
NC	3:2:2 - 1	0	1

CONCLUSIONS

It is suggested that the number of angular foramina in *Jaculus* is a matter of random individual variation, often differing in the two mandibles of an individual. It is further suggested that pallid or darker dorsal coloration and sole brushes are in reality related to substrate coloration in *Jaculus* and represent the effect of selection in producing "sub-

strate races" more or less protected by cryptic resemblance to the predominant substrate, as has been well demonstrated in the three-toed jerboa and many other desert rodents (Harrison, 1975). The concept of two sibling species within *Jaculus jaculus* populations on the basis proposed by Ranck (1968) is rejected.

ACKNOWLEDGMENTS

The author is much indebted to J. Edwards Hill and staff of the Mammal Section, British Museum (Natural History), for kindly providing facilities to examine material of *Jaculus* in the National collection and to all those who have donated material of this species to the Harrison Zoological Museum, including T.

Bickley, P. A. Clancey, M. D. Gallagher, D. Grant, J. G. Harrison, H. Hovel, S. Howe, M. K. Lambert, M. Legg, R. E. Lewis, T. D. Rogers, G. B. Stafford, S. Seligman, and Sheikh Zaid bin Sultan.

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ENERGETICS OF SURVIVAL IN *HETEROCEPHALUS GLABER* (RÜPPELL), THE NAKED MOLE-RAT (RODENTIA: BATHYERGIDAE)

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ABSTRACT

Heterocephalus glaber, a colonial mole-rat, has a highly structured social system with a worker and non-worker class and a dominant breeding female. Recruitment rates for the colony and growth rates of the young are very low. Unusual features in its physiology (a high rate of thermal conductance, a low basal metabolic rate, a low body temperature, and poor ability to ther-

moregulate) have in the past been regarded solely as adaptations to the high temperature and humidity of the burrows in which mole-rats live. It is here suggested that food is limiting to *Heterocephalus* and that many of its unusual features can be attributed to the need to maintain a low energy budget for the colony.

INTRODUCTION

Heterocephalus glaber, the naked mole-rat is a small colonial rodent with an average weight of about 35 g. It occurs in arid regions of Kenya, Ethiopia, and Somalia—areas characterized by a low mean annual temperature amplitude, diurnal ambient temperatures of above 27°C, and an annual rainfall of less than 700 mm. Vegetation in these areas is sparse and many plants have swollen subterranean portions; these form the main food for *Heterocephalus*.

Heterocephalus lives underground in a burrow system, which consists of extensive foraging burrows running at root or tuber level and a deeper nest area. The ground is very hard and the burrows semipermanent (Jarvis and Sale, 1971). The tubers and bulbs, on which they feed, are found by the energetically expensive method of extending the foraging burrows in an apparently random direction until food is encountered. From the burrow pattern, it appears that once a tuber has been located, the neighborhood is then searched thoroughly—seemingly in response to the fact that many tubers reproduce vegetatively and tend to occur in patches. Once located, large items of food such as tubers are left growing and are gradually hollowed out by the mole-rats, small food items are carried to the nest area and eaten there.

The microclimate in all but the very superficial portions of the burrow system is extremely uniform, with humidities (usually) above 90% and temperatures between 30 and 32°C. The mole-rats avoid extreme temperatures in the superficial burrows by restricting their burrowing activities to early morning and late afternoon.

Heterocephalus has a skin that is hairless, except for scattered sinusoidal hairs all over the body; it

is well vascularized but lacks sweat glands and the normal mammalian layer of subcutaneous fat (Thigpen, 1940). Consequently, these mole-rats have very high rates of thermal conductance (McNab, 1966). In laboratory studies on single naked mole-rats, McNab (1966, 1968) found them to have a metabolic rate that was less than 40% of that expected, a body temperature of about 32°C, and the poorest capacity for thermoregulation of any known mammal. My own findings confirm these observations (Withers and Jarvis, in preparation). McNab suggests that these modifications reduce the probability of overheating in an environment where evaporative and convective cooling are greatly reduced.

All previous physiological studies on *Heterocephalus* (McNab, 1965, 1966, 1968) have been confined to isolated animals. However, my observations on captive colonies of naked mole-rats have shown them to be highly social rodents. Members of the colony have specific roles in that there are worker and non-worker classes and a dominant breeding female. Furthermore, mutual contact and huddling are important to the mole-rats. I, therefore, suggest that any explanation of their physiology, which does not consider their sociality as well as more aspects of their habitat than just temperature, will at best only give partial answers to the questions raised. This paper attempts to summarize and synthesize our present knowledge of the ecology, physiology, and ethology of these mole-rats and to suggest ways in which these have been influenced by the environmental pressures to which these mole-rats are subjected. More detailed accounts of their social structure and of the physiology of grouped and not single mole-rats will be published later.

MATERIALS AND METHODS

Naked mole-rats were caught by opening a foraging burrow and pushing a spade down behind any animal coming to investigate the damaged burrow. Because of this method, only the worker class of mole-rats were caught. Monthly samples of approximately 30 mole-rats were caught in this way at Mtito Andei, Kenya (240 km southeast of Nairobi), over a complete calendar year. From these animals data on body measurements, reproductive condition, and stomach contents were obtained.

Fifty live mole-rats were collected in the same way at Mtito Andei in early 1974 and established in three "colonies" in the laboratory in Cape Town. After approximately one year each colony had established its social hierarchy and individuals from one colony were marked with subcutaneous injections of India ink, to enable a more detailed study of the social structure of a colony. The two other colonies were used in physiological studies and left undisturbed for breeding.

The preferred ambient temperature range of *Heterocephalus* was determined by establishing a temperature gradient (21°C to 40°C) in a terrarium housing one of the colonies and observing the temperatures selected by single and huddling members of the colony. Observations were made at 10 min intervals and the number of mole-rats sleeping singly or huddled was noted.

Emphasis in the physiological studies was placed on the responses of the mole-rats to a temperature range that approximated the normal burrow temperature. The temperature selection studies, and also field measurements, suggested that the normal burrow temperature lies close to 32°C. McNab (1966)

demonstrated that, below 20°C and above about 36°C, *Heterocephalus* almost completely abandons any attempt to thermoregulate—again suggesting that these temperatures lie outside those normally experienced by the mole-rats. For these reasons, my investigations into the effect of temperature on the metabolic rate of *Heterocephalus* were limited to ambient temperatures lying between 20°C and 34°C.

For the metabolic studies, mole-rats were placed in clear perspex containers in a constant temperature chamber. Dried air was drawn through the containers at a known flow rate, which could be varied to suit the experimental temperature and the number of mole-rats in the container. Samples of air were drawn off the air stream and these were analyzed in a Beckman oxygen analyzer OM-1L. The activity of the mole-rats and the chamber temperature was monitored throughout the experiment. At the end of each experiment, the rectal body temperature of each mole-rat was taken using a Bailey Bat-4 laboratory thermometer with attached microprobe. The environmental temperatures used were 20°C, 25°C, 30°C, and 34°C, with the mole-rats in groups of four or singly. The mole-rats were not postabsorptive when placed in the chamber; the emphasis of this study was on determining the responses of mole-rats under as normal a situation as possible. Mole-rats feed intermittently throughout the day and experimental animals were removed from the colony as required. It is highly likely that the animals used in successive experiments were at about the same absorptive stage.

RESULTS

Social Organization

The social structure of the established colony consisted of a single dominant female weighing 53 g, ten mole-rats of both sexes forming the working class and with an average weight of 32 g, and three non-working mole-rats (two males and one female) with an average weight of 38 g. A similar distribution of numbers and sizes appeared to be the pattern in the other two captive colonies.

The dominant female suppresses breeding in all the other females in the colony. Before the social hierarchy was completely established in the captive colonies, females coming into estrus at the same time would fight each other, frequently resulting in death for one of them. In the established colonies, this situation never arises and high intensity aggression is never seen. The breeding female is dominant over all other mole-rats in the colony. She initiates courtship and will solicit any male in the colony. However, it is not yet certain whether all males successfully copulate with her. Removal of the dominant female results in another mole-rat assuming the dominant role. This animal appears to come from the non-working mole-rats, but, as is evi-

denced by the fact that my colonies were established from working class animals, the potential for breeding appears to lie latent in all the females of the colony.

The litter size of mole-rats born in captivity ranged from three to 11 young. Death of a newborn litter may lead to the dominant female breeding again. However, if the young survive, the female appears to breed only once a year. One captive female produced three litters and a total of 24 young within a period of 6 months, only the last litter survived and she has not bred again for 11 months. In the field, breeding appears to be associated with the rainy season (Jarvis, 1969) and it is possible that in unusually good years a litter may be born in both the long and short rains. Growth rates of the young are exceptionally slow, with juveniles taking at least a year to attain adult size (Fig. 1). In spite of their slow maturation rates, the young mole-rats join the worker class at the age of 2 to 3 months.

The non-working mole-rats are the next largest animals in the colony. They remain within the confines of the nest area and are only seen when they emerge to urinate or defecate. Their role in the col-

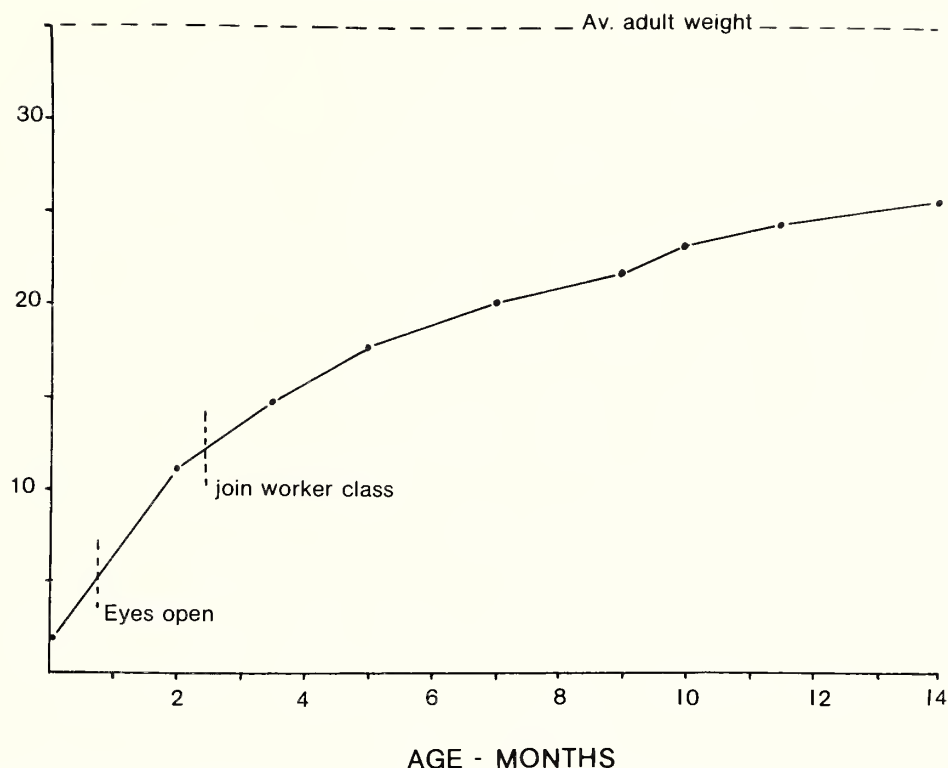


Fig. 1.—The mean growth rate of *Heterocephalus* born and reared in captivity. Compiled from data from two litters (seven mole-rats).

ony appears to be to huddle with the dominant female. It is probable that they are also the most fit to reproduce and that only these males successfully copulate with the dominant female. It is also possible that if the colony numbers are seriously depleted, or if the rains have been exceptionally good, the non-working female(s) may also breed.

The working class mole-rats make up the remainder of the colony, appear to be of an equal sex ratio, and comprise the smallest animals in the colony. The females are non-breeding, but many of the males appear to be potentially capable of breeding in that sperm are produced and they attempt to mount the dominant female when she is in estrus. In the monthly samples collected at Mtito Andei no pregnant or parous females were found in a total of over 150 animals, whereas many of the males had spermatozoa in their vasa deferentia, indicating that the situation found in the captive colony does reflect field conditions.

The working class mole-rats are responsible for the digging of the burrow system, location of the food, transport of food to the non-working animals, and for carrying nest materials to the nest. A high

degree of cooperation is shown within this class when they are digging (Jarvis and Sale, 1971). Mutual coprophagy also occurs with the recipient mole-rat (frequently from the non-working class) begging feces from a donor mole-rat.

The smaller size of the working class mole-rats is partly due to the fact that young animals are incorporated into this class at an early age. However, my evidence suggests that the growth rate of these working animals is also retarded. All members of the colony studied were at least 3.5 years old and this size difference was still apparent. Furthermore, the average weight of the whole captive colony is comparable to that of an almost complete colony of 39 mole-rats collected recently at Mtito Andei. These two facts suggest that this size difference is an inherent part of the colony structure.

Another characteristic of the colony is the importance of mutual contact. This appears to be essential for the well-being of the mole-rats and, if forcibly separated from the remainder of the colony, a mole-rat is restless and its overall condition deteriorates. Prior to sleeping, mole-rats frequently seek other members of the colony and, depending

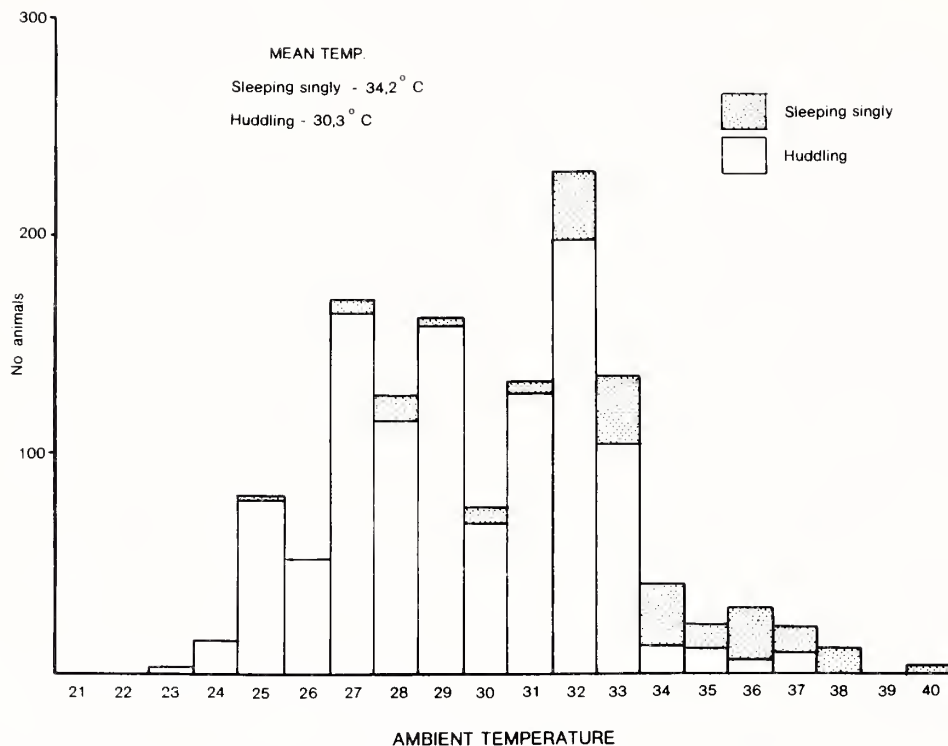


Fig. 2.—Temperature selection in resting *Heterocephalus*. Observations were made at 10-min intervals and the number of animals resting singly or huddled at the different temperatures in the gradient are noted.

on the ambient temperature, either huddle with them or lie close to them. The lower the ambient temperature, the greater the tendency to huddle. This sociality is in marked contrast to the majority of other species of mole-rats, which are solitary aggressive rodents.

It should be stressed here that these observations on the social structure of *Heterocephalus* colonies should, at present, only be regarded as indications of what might be true for the species. More detailed laboratory studies on an almost complete colony of mole-rats captured in October 1977, are at present underway.

Temperature Selection and Metabolic Rates

From the temperature selection studies (Fig. 2), it can be seen that single resting mole-rats generally choose temperatures of between 32 and 38°C with a mean of 34°C. What is not shown in Fig. 2 is the duration of stay at these temperatures. Continuous observations on selected single animals demonstrated that the visits to the higher temperatures tended to be fairly brief and once the mole-rat had "warmed-up" it selected a lower temperature for sleeping. Huddling mole-rats favored temperatures

of between 25°C and 33°C in which to sleep (mean 30°C). It can be seen that the temperatures selected by *Heterocephalus* correspond closely to the burrow temperatures of 30°C to 32°C measured in the field. Fig. 2 also clearly demonstrates the strong preference of *Heterocephalus* for huddling rather than solitary sleeping.

From Fig. 3, it can be seen that physiologically, the optimum ambient temperatures also lie close to the normal burrow temperature range. There is a marked reduction in the metabolic rates of mole-rats at 30°C and 34°C and a sharp increase at lower temperatures.

Also apparent from Fig. 3 is that throughout the temperature range studied, there is a significant difference between the metabolic rates of mole-rats resting singly and those huddling. This difference is most marked at 25°C and 30°C where the metabolic rates of the groups of four huddling mole-rats are half of those of the single animals.

At 34°C, the resting metabolic rate of the huddling mole-rats is close to the basal metabolic rate found by McNab (1966) and this temperature falls within the very narrow thermal neutral zone of these mole-rats. McNab (1966) has shown that

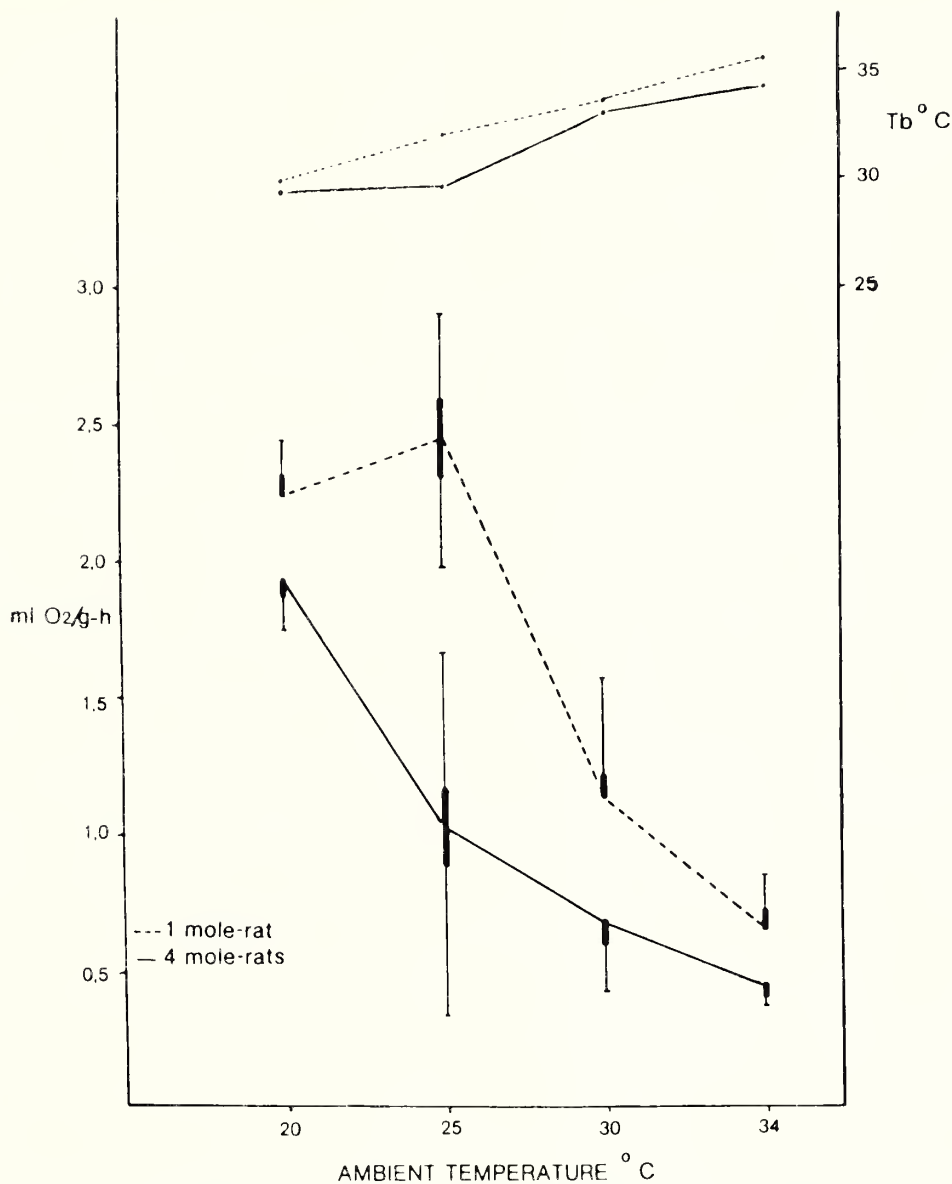


Fig. 3.—The metabolic rates and rectal body temperatures of *Heterocephalus* resting singly or huddling in groups of four, at different ambient temperatures. Standard deviation and standard error are indicated for the metabolic rates. The difference between the metabolic rates of single and huddling mole-rats is significant ($P = .001$ for 25°C and 30°C; $P = .01$ for 20°C and 34°C).

above 34°C and below 31°C the energy cost to the animal increases very steeply. My own findings confirm this for the lower temperatures.

The ability of *Heterocephalus* to thermoregulate is limited. The increased oxygen consumption with decreasing temperature and body temperatures el-

evated above ambient shown in Fig. 3 suggest that although these animals are thermolabile, they show some thermoregulatory ability within the temperature range studied. Outside these temperatures, McNab (1966) found *Heterocephalus* to have a rapidly diminishing ability to thermoregulate.

DISCUSSION AND CONCLUSIONS

The temperature selection studies, environmental measurements, and the narrow ambient tempera-

ture range over which *Heterocephalus* appears to thermoregulate and within which oxygen consump-

tion is minimal, all suggest that the naked mole-rat lives in an environment in which temperature fluctuations are minimal. They also suggest that although the burrow temperatures and humidities are fairly high, these mole-rats are rarely exposed to potentially lethal temperatures. Extremes of temperature are only encountered in very superficial burrows and these are avoided by *Heterocephalus* when temperatures are unfavorable. For these reasons, I feel it necessary to look for largely non-thermoregulatory reasons for their unusual physiology and social structure.

I would suggest that food is limiting to *Heterocephalus*. These mole-rats live in semidesert regions where most of their food is in the form of scattered tubers, which, unlike much annual vegetation and grasses, are slow to respond to favorable rainfall. The food supply, although low, is at the same time fairly predictable and it appears that selection in both the physiology and social structure of *Heterocephalus* has favored features, which result in a low but steady demand by the colony.

The colony is so structured that the more expendable mole-rats form the worker class and are involved in the energetically costly search for food. For maximal efficiency these animals do not breed. A limited few of the largest and probably the most genetically fit members of the colony reproduce and remain in the most protected part of the burrow system. These animals are waited on by the other members of the colony and they can therefore channel all their energy into reproduction. They would also huddle with each other and further lower the metabolic cost of living.

For the worker mole-rats, the largest expenditure of energy is in locating the patches of tubers. Once one tuber has been found, the chances of others occurring in the neighborhood are high and the whole area can be exploited with little additional cost to the colony. Evidence from the field suggests that burrowing activities (as indicated by an increased production of mole-hills) are heightened following the rains when the soil is softer and more easily worked than during the dry season. It therefore appears that *Heterocephalus* concentrates its major food finding activities into the most energetically favorable times of the year. The tubers thus located are left growing and exploited as the colony has need of them.

It seems probable that in semidesert areas a colony of mole-rats has a greater chance of surviving than a single animal. In the colony, the cost of bur-

rowing can be shared by the working animals and the chance of locating clumps of tubers enhanced by having more than one animal searching the area. If the colony size is large enough, the search for food can be undertaken on several fronts at the same time. Obviously, there must be an optimum number of worker members to the colony; too many would rapidly exhaust the food found and too few would decrease the chances of finding the food sources.

The burrow systems are extensive and frequently over 100 m long. Distances between tuber patches also appear to be considerable. When a long burrow system has to be dug, a small body size is advantageous in that burrow diameter can be kept to a minimum and the volume of soil displaced and the associated energy cost to the colony kept as low as possible. It is interesting therefore to find that *Heterocephalus* is the smallest of the rodent moles.

Unlike the majority of rodents of similar size, the number of naked mole-rats within the colony appears to remain stable. This is evidenced by the low recruitment rates, limited breeding season, the low growth rates of the young, and the high longevity of the members of the colony (many of my captive animals are at least 5 years old). With this situation, it would appear that at no time of the year would there be a heavy demand on the energy reserves of the colony. Emphasis throughout is on a low but steady demand—a situation well suited to the steady but limited food resources available to the colony. A stable population size also lends itself to the development of a colony where a high degree of social structuring is possible.

McNab (1966) suggests that because of a reduced potential for evaporative and convective cooling in the hot humid burrows in which *Heterocephalus* lives, there may be periods when there is considerable heat storage by the mole-rats, especially when digging. A low metabolic rate and high thermal conductance would reduce the probability of overheating. Although this may well be true, these features may also be linked to their limited energy resources. A metabolic rate that is less than 60% of the expected rate would considerably reduce the daily energy budget of the mole-rats and high rates of thermal conductance open the way to low-cost behavioral thermoregulation.

The possibility that a low metabolic rate is linked to energy conservation was dismissed by McNab because he found that the lower limit of thermoneutrality (31°C) in *Heterocephalus* lay above his

mean burrow temperature measurements (30°C). Because of the small size of *Heterocephalus* and their high rates of thermal conductance, this would lead to a marked increase in energy expenditure above the basal level. He argued that if energy conservation was important, there should have been a broad overlap between the burrow temperature and the zone of thermoneutrality.

My measurements of burrow temperatures, during the height of the dry season, gave readings of above 31°C suggesting that, at certain times of the year, burrow temperatures do lie within the zone of thermoneutrality. My studies also suggest that, should the burrow temperature fall, *Heterocephalus* can reduce its rate of thermal conductance, and thus extend its lower limit of thermoneutrality, by huddling. Furthermore, it is possible for *Heterocephalus* to utilize behavioral thermoregulation when temperatures are lower or higher than preferred by simply moving to areas in the burrow sys-

tem, which have a more favorable temperature. Thus, if heat stressed, the mole-rats could move to deeper and therefore cooler parts of the system where they can off-load heat passively. If too cold, movement to more superficial parts of the burrow during the daylight hours and the early evening would often bring the mole-rat to warmer parts of the system and the animal could again employ passive means to raise its temperature.

Therefore, this evidence suggests to me that here we have a rodent whose physiology, social organization, and behavior have all been influenced by the harsh environment in which it lives—an environment where temperatures are high and food appears to be a limiting factor. An understanding of the ethology and social organization of these mole-rats, and the linking of these with their physiology, suggests that both temperature and food resources must be considered when seeking an explanation for the unique features found in *Heterocephalus*.

ACKNOWLEDGMENTS

I am grateful to Dr. P. C. Withers and Mr. R. Bally for allowing me to draw on data on the physiology and temperature selection of *Heterocephalus*, to be published later, jointly.

Dr. Peter and Mrs. Heidi Bally of Nairobi, Kenya, have given

me invaluable assistance on numerous occasions both in sending me live *Heterocephalus* and in assisting me in my field work; my very sincere thanks go to both of them.

My thanks also go to Mrs. S. Hardman for typing this paper.

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MODELING OF THE POPULATION CYCLES OF TWO RODENTS IN SENEGAL

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ABSTRACT

Models of adaptive strategy to periods of decreasing populations in two rodents in Senegal are given. Actual densities of *Mastomys erythroleucus* and *Taterillus gracilis* are compared mathematically to observed densities. Differences in various

ecological parameters of the two species account for their respective adaptive success during periods of low population densities.

INTRODUCTION

The two principal species of rodents—*Mastomys erythroleucus* (Temminck) (Rodentia, Muridae) and *Taterillus gracilis* Thomas (Rodentia, Gerbillidae)—present after the population outbreak of 1975–1976 in the Bandia region of Senegal (14°37'N, 17°01'W), were studied from November 1975 to August 1977. This study particularly involved the large population decrease after the 1975–1976 outbreak. Results

are given for the different habitats together—a dry deciduous woodland, some areas of it cut for charcoal production and adjacent areas under cultivation. Different soils are present in Bandia, but all the areas included in this study are on tropical lateritic soils. A further description of the area was presented by Hubert (1977).

METHODS

A large number of animals (more than 1,500 individuals) were caught in snap traps (60 traps during four nights/week in four different habitats) and in 500-m-long lines consisting of 50 live-traps of iron wire (type Manufrance) placed every 10 m. Specimens were autopsied to determine their sexual activity (particularly the number of young in the litter of the females, which varies during the breeding period increasing at first and then decreasing, Table 1). The eye lenses were taken and dried for weighing to determine the age of the individuals collected, by comparison with a diagram established from rodents in captivity (Hubert and Adam, 1975). Thus the approximate dates of birth of each generation are known.

From August 1976, an area of 600 m by 1,000 m was trapped twice each month with 160 traps in rotation and two plots of 4 ha each were trapped every 1.5 months by mark-and-release method, with a 10 m by 10 m grid of 441 live traps of iron wire (type Manufrance). The first trapping allowed determination of the density by CMR method during 10 days. The subsequent trapping (five nights every 1.5 months) allowed the monitoring of the marked population, estimation of the densities, and the distinction between migrations and mortality. Thus a monthly death rate was estimated for different periods; it varied according to the density and to possible epizootic disease being present. The death rate is calculated by the difference between the "load of living animals on the area" at one trapping period and at the

following one, that is, the number of the formerly marked animals increased by the newly marked, which will be recaptured later and an average number of "residents" animals representative of the animals crossing the area during the trapping period. This loss could be interpreted as the death rate for a large enough area (where the number of entering rodents is equivalent to the departures) and when the calculation is made with the overall data for different environments taken together. A disease could have occurred from October to December 1976; in fact, a virus ("Bandia" virus, isolated from ticks and one *Mastomys* 10 years ago) was discovered again in January 1977 in four species present in Bandia, after a large population decrease. Its lethal effect has been demonstrated in the laboratory on *Mastomys erythroleucus* by the death of all the young in 10 days. Experiments are in progress for the other species.

A mathematical formula has been adjusted for modeling the population cycle of rodents in terms of the following data, that is, number of young in each litter, mean date of birth of each generation, and monthly death rate for each period. Terms for the formula are as follows: $P(t)$, the population at time t (in days); P_0 , the population at time $t = 0$; M , the monthly death rate ($0 \leq M \leq 1$); \bar{n}_i , the average number of young for the i^{th} litter; T_i , the date (in days) of the i^{th} litter. The sex ratio is supposed to be 1.0.

For *Mastomys erythroleucus*, a Hewlett Packard HP 65 com-

puter was employed, using the formula:

$$P(t) = P_0 10^{\frac{t}{30} \log(1-M)} + \frac{P_0 \bar{n}_1 10^{\frac{T_1}{30} \log(1-M)}}{2} \cdot 10^{\frac{t-T_1}{30} \log(1-M)} \\ + \frac{P_0 \bar{n}_2 10^{\frac{T_2}{30} \log(1-M)}}{2} \cdot 10^{\frac{t-T_2}{30} \log(1-M)} \\ + \frac{P_0 \bar{n}_3 10^{\frac{T_3}{30} \log(1-M)}}{2} \cdot 10^{\frac{t-T_3}{30} \log(1-M)} \\ + \frac{\bar{n}_4}{2} \left[P_0 10^{\frac{T_4}{30} \log(1-M)} + \frac{P_0 \bar{n}_1 10^{\frac{T_4-T_1}{30} \log(1-M)}}{2} \right] \cdot 10^{\frac{t-T_4}{30} \log(1-M)}$$

The formula is not simplified, as it was used for the programming of the HP 65. The evolution of the different generations is given by the same program, where $\bar{n}_2 = \bar{n}_3 = \bar{n}_4 = 0$, and so on.

For *Taterillus gracilis*, it is not possible to use the same program because too many generations occur in the same year (nine from August 1975 to August 1976). In this case we used the following formula (example from May 1975 to August 1976):

$$P(t) = P_0 F + \frac{\bar{n}_1}{2} P_{06} F + \frac{\bar{n}_2}{2} (P_{06} + P_{03}) F + \frac{\bar{n}_3}{2} P_0 F \\ + \frac{\bar{n}_4}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) \cdot F + \frac{\bar{n}_5}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) \cdot F \\ + \frac{\bar{n}_6}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) \cdot F + \frac{\bar{n}_7}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) \cdot F \\ + \frac{\bar{n}_8}{2} \left[P_0 + \frac{\bar{n}_1}{2} P_{06} + \frac{\bar{n}_2}{2} (P_{06} + P_{03}) \right] \cdot F \\ + \frac{\bar{n}_9}{2} \left[P_0 + \frac{\bar{n}_1}{2} P_{06} + \frac{\bar{n}_2}{2} (P_{06} + P_{03}) + \frac{\bar{n}_3}{2} P_0 \right] \cdot F \\ + \frac{\bar{n}_{10}}{2} \left[P_0 + \frac{\bar{n}_1}{2} P_{06} + \frac{\bar{n}_2}{2} (P_{06} + P_{03}) \right. \\ \left. + \frac{\bar{n}_3}{2} P_0 + \frac{\bar{n}_4}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) + \frac{\bar{n}_5}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) \right. \\ \left. + \frac{\bar{n}_6}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) + \frac{\bar{n}_7}{2} \left(P_0 + \frac{\bar{n}_1}{2} P_{06} \right) \right] \cdot F$$

$$\text{where: } F = 10^{\frac{t}{30} \log(1-M)}$$

Table 1.—*The main reproductive data for Mastomys erythroleucus and Taterillus gracilis in the Bandia area during the 1975–1976 and the 1976–1977 breeding periods.*

Species	Approximate date of each generation	Average number of young per litter	Participation of young in breeding
<i>Mastomys erythroleucus</i>	1 November 1975	8	–
	1 December 1975	13	–
	12 January 1976	13	–
	28 February 1976	10	+
	1 October 1976	8	–
	1 November 1976	10	–
	1 December 1976	13	–
<i>Taterillus gracilis</i>	10 May 1975	3	–
	20 August 1975	3	–
	15 September 1975	4	–
	1 November 1975	4	–
	5 December 1975	5	–
	30 December 1975	5	–
	25 January 1976	5	–
	25 February 1976	3	–
	25 March 1976	3	–
	5 May 1976	1	+
	20 August 1976	3	–
	25 September 1976	4	–
	25 October 1976	5	–
	25 November 1976	5	–
	20 December 1976	5	–
	20 January 1977	5	–
	30 March 1977	3	+

P_{06} is the number of animals older than 6 months in P_0 ; P_{03} is the number of animals between 3 and 6 months old in P_0 . We know $P(464) = 6$; a sample of *Taterillus* caught at $t = 0$ gave the population structure (dry crystalline lens weight), so we know also $P_{06} = f(P_0)$ and $P_{03} = f(P_0)$ and now we can compute P_0 ; P_0 known, we can compute $P(t)$ from $t = 0$ to 464 days. The observed density (by CMR method) of August 1976 is used as the basis of all the calculation for the two species.

RESULTS

The two graphs (Figs. 1 and 2) present the following data: The total fluctuations in the number of animals present per hectare at time t ; the trapping population at time t , consisting of adults and recently weaned young; the appearance and growth of each litter until the disappearance of all its individuals; the ratio of each age group in the population at time t .

It is easy to see that if the actual densities of the two populations are now equivalent and close to the observed densities, they did not have the same previous development.

Mastomys erythroleucus accounted for a large portion of the population outbreak of 1975–1976, and its densities were very high during the last year. The possible occurrence of an epizootic disease (or

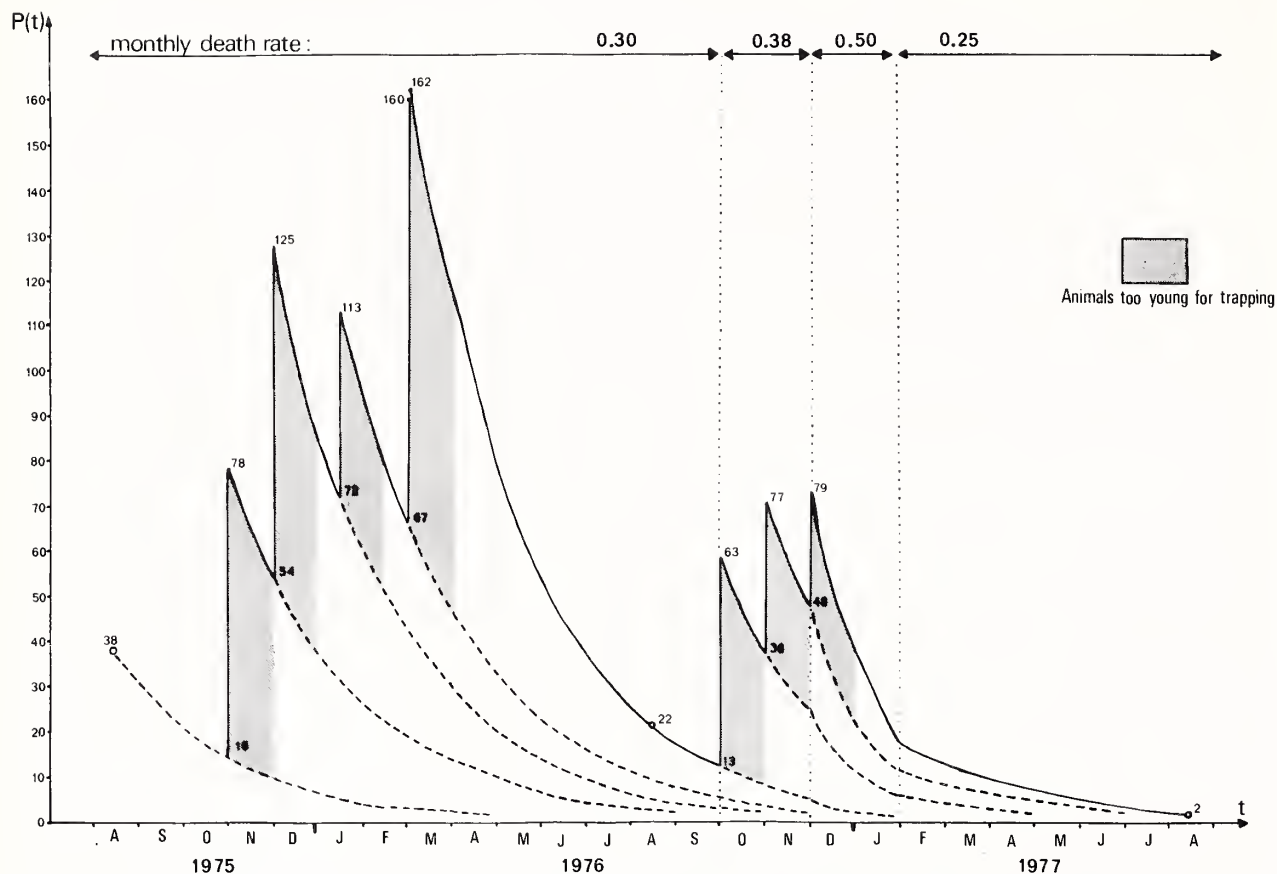


Fig. 1.—Fluctuations in the population level of *Mastomys erythroleucus* on 1 ha near Bandia, Senegal.

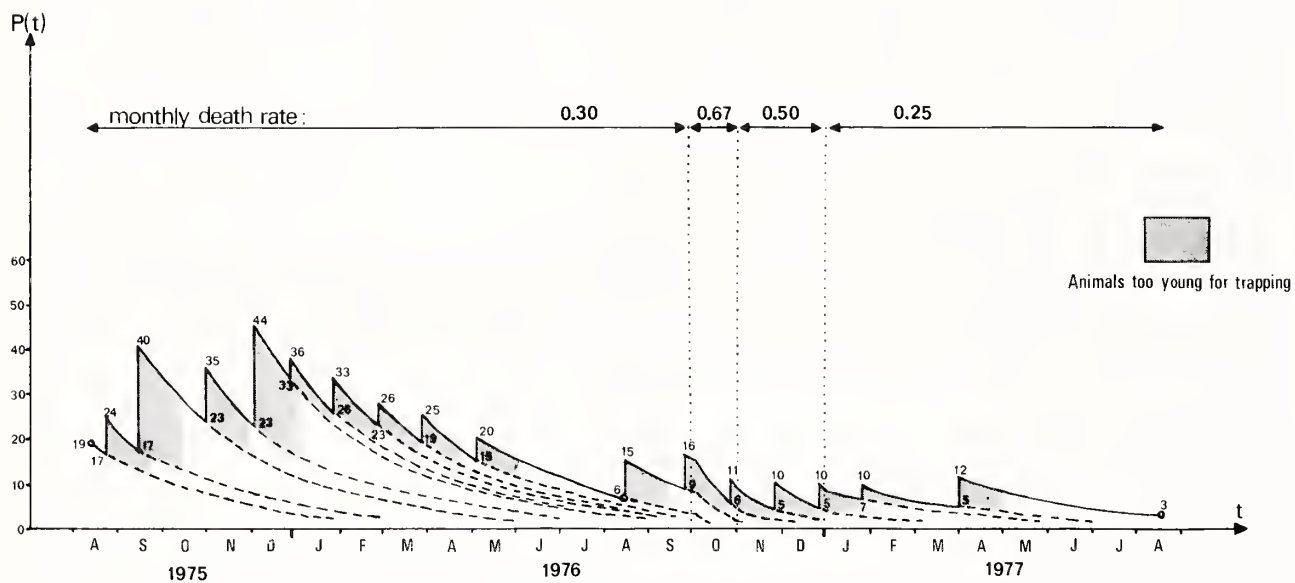


Fig. 2.—Fluctuations in the population level of *Taterillus gracilis* on 1 ha near Bandia, Senegal.

a different factor increasing the death rate) reduced the population considerably to the actual rate in spite of large reproduction. Mortality of the adults was high, and that of the young was such that the first litters, which had bred at the end of the breeding period in 1975–1976, could not do so in 1976–1977.

Although the densities of *Taterillus gracilis* were relatively high in 1975–1976, there was no popula-

tion outbreak of this species. Densities were almost unchanged and less subject to variations during that year because of a longer breeding period and a higher individual survival rate. However, the *Taterillus* population was also affected by the disease, as the monthly death rate increased considerably and the population remained in the fields only because of the continuation of the breeding period late in the year.

DISCUSSION

Once more the difference of adaptative strategy appeared between *Mastomys* and *Taterillus* populations as discussed below.

Mastomys erythroleucus.—This species has a short breeding period, but with large litters (eight to 13 young per litter), allowing the population to reach a very high level. This large production of young animals permits colonization of new environments, as described by Hubert (1977). They also possess resistance to various disasters (drought, diseases) and the ability to exploit the environment when the production of young is highest, as in the beginning of the dry season. These young animals supply the parental generation for the next year.

Taterillus gracilis.—The breeding period of this species continues for a longer time; it begins earlier in the wet season and continues later into the dry season, with the largest participation of the young animals. The fertility rate is lower than in *Mastomys*; three to five young are produced per litter according to the period of the breeding season. Populations are more regularly present in the fields than those of *Mastomys* and they resisted the disease by maintaining an almost standard breeding period in

1976–1977. The individuals of this species that live more than one year are more numerous than in *Mastomys*, thereby maintaining the population in large areas.

For this computation, the death rate was supposed to be constant throughout the life of the animals, and all the females older than 6 months, or 3 months if the young females do participate to the breeding period, are supposed to be littering at each generation. These two hypotheses do not contradict the observed data. Using observed densities in August 1976 as the basis of calculation, the expected densities obtained for August 1977 are very close to the observed ones for the same period (that is, about two individuals per ha for each species).

The resemblance between observed and computed data allows us to do the same calculations on the fluctuations of the densities. This model can also be used for the calculation of productivity by estimating the complete number of rodents produced, including the juveniles too young to be trapped.

This work has been carried on with a financial support of the C.N.R.S., contract no. 1 651-2294-ATP "Dynamique des populations."

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RADIO-TRACKING OF A SMALL RODENT, *HYBOMYS UNIVITTATUS*, IN AN AFRICAN EQUATORIAL FOREST

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ABSTRACT

Preliminary studies of home range, activity periods, and movement in *Hybomys univittatus* (Mammalia: Muridae) was studied by using radio-tracking. Comparisons between males and

females indicate males have larger home ranges and are generally more restricted to them than females. Both sexes are diurnal in their periods of activity but females are less active than males.

INTRODUCTION

Most small rodents are easily caught in live-traps. However, it is often difficult to watch them in the field, especially in closed biotopes. Therefore, since 1975, I have used a radio-tracking technique (transmitter AVM, SM1 type; telemetry receiver model LA 12, with Yagi antenna).

I have been working for two years in the Central African Empire, near M'Baiki. These preliminary results concern a diurnal murid, *Hybomys univittatus* (Peters, 1876).

This mouse measures 100 mm in length of head

and body and weighs 50 to 70 g. The fur is soft. The dorsal color ranges from light yellowish brown to dark brown, with a black middorsal stripe that extends from the nape to the base of the tail. The ventral color ranges from tawny to grayish white.

This rodent species is only terrestrial. It lives in burrows in which it builds nests made of twigs. An individual may have three or four burrows but one is more often occupied than the others. *Hybomys* is solitary in its burrows.

METHODS

Experimentation

Ten *Hybomys*, six males and four females of various ages, have been observed by the radio-tracking technique during December 1975, January, April, and May 1976, and January, February, April, and May 1977; that is to say in the dry season and the beginning of the rainy season.

During these observations, one female aborted its young; two animals, male and female, lost their transmitters (the female was just leaving its home range); finally, a male died of a wound made by the antenna-collar that it had been carrying for 3 weeks. The transmitter weighs 12 g with its wrapping.

Environment

These observations were made in a dense equatorial forest in the process of secondary seral stage. There the underwood is dense and the ground is covered with branches and trunks of dead trees intermixed with creepers.

An area of 10,000 square m has been gridded with narrow cross-trails at 20-m intervals, to compensate for the weak range of the transmitters. These cross-trails have been just roughly cleared, to reduce reluctance in the rodents to cross them. At each crossing a Sherman trap or a Saint-Etienne trap was placed. The rodents caught by this method have been marked by toe-clipping and thus it has been possible to watch them year round. The most assiduous visitors to the live-traps were selected to carry a transmitter; this selection increases the chance of recovering the instrument later.

RESULTS AND DISCUSSION

Home Range of Hybomys

Captures and recaptures gave us information about the home range of *Hybomys*. From radio-tracking, it has been possible to delimit the areas more exactly. They vary from 4,500 to 6,100 square m for the cases of males and from 1,400 to 1,800 square m for females.

A male spends its entire adult life (about 12 months) in the same home range. When the individual dies, its home range remains vacant for a while, but within a few weeks or months, another male or a female will take possession of the area. The limits of the new individual's home range will not be exactly the same as those of the previous one, particularly if the new individual is a female.

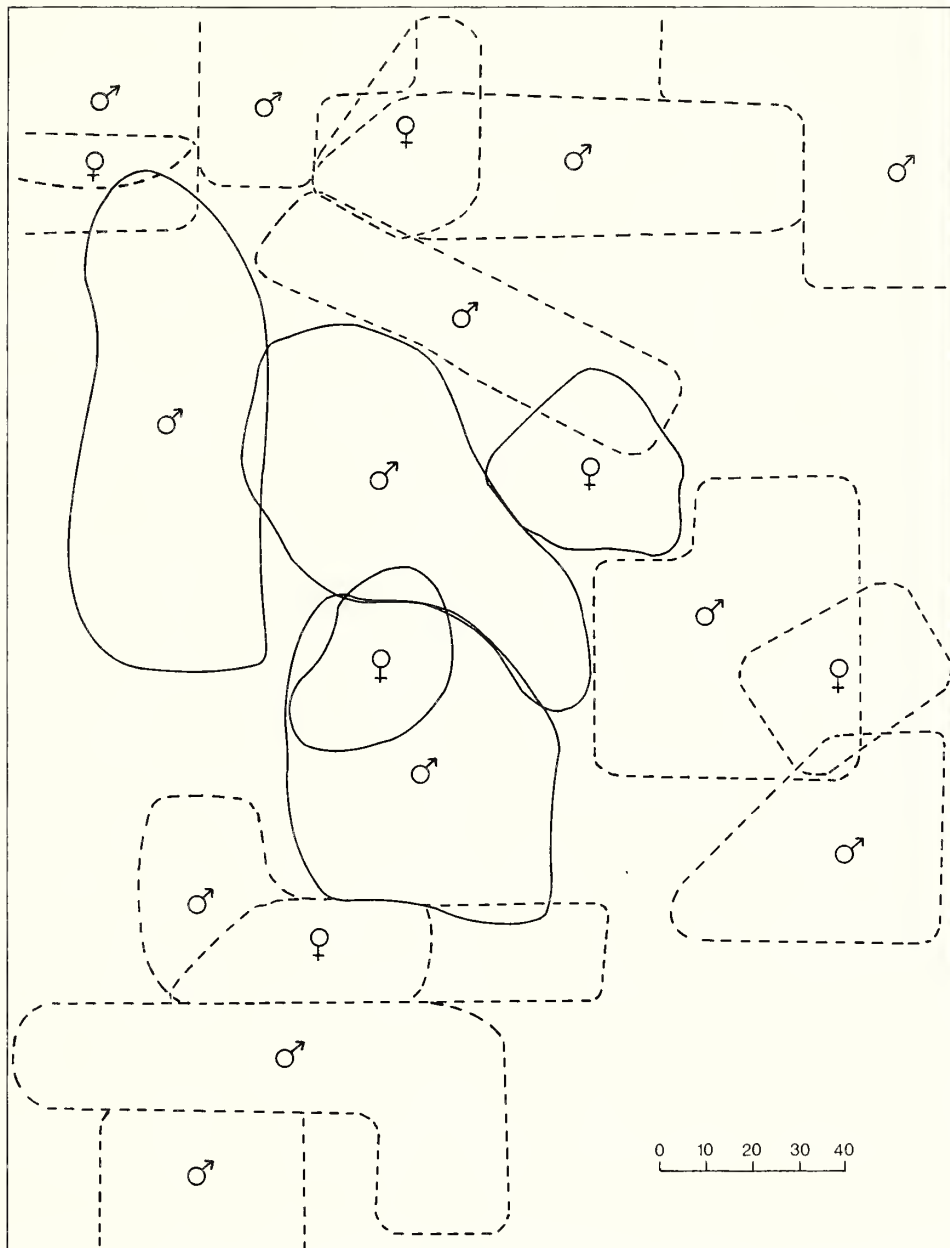


Fig. 1.—Home ranges (in meters) of male and female *Hybomys univittatus* from January to May 1976. Four home ranges were calculated from results of the radio-tracking technique. Broken lines indicate the home ranges defined by the "capture-mark-and-release" technique.

The home ranges of neighboring males do not overlap. If one of the males dies, its neighbor can enlarge its own home range but this enlargement is always moderated. Only the young *Hybomys* can move from one home range to another, contributing to the species dispersal. For instance, a young female left its home range and lost its transmitter at 280 m from its burrow. This distance represents seven times the width of its home range. The animal

certainly went farther than that because we never caught it again.

Males do not tolerate other males in their home range. If two males come together, the owner gives chase to the other individual and bites it cruelly if owner overtakes the intruder. Some males share their home range with one or two females, which occupy smaller areas (see Fig. 1). It might happen that the female who lives with a male during some

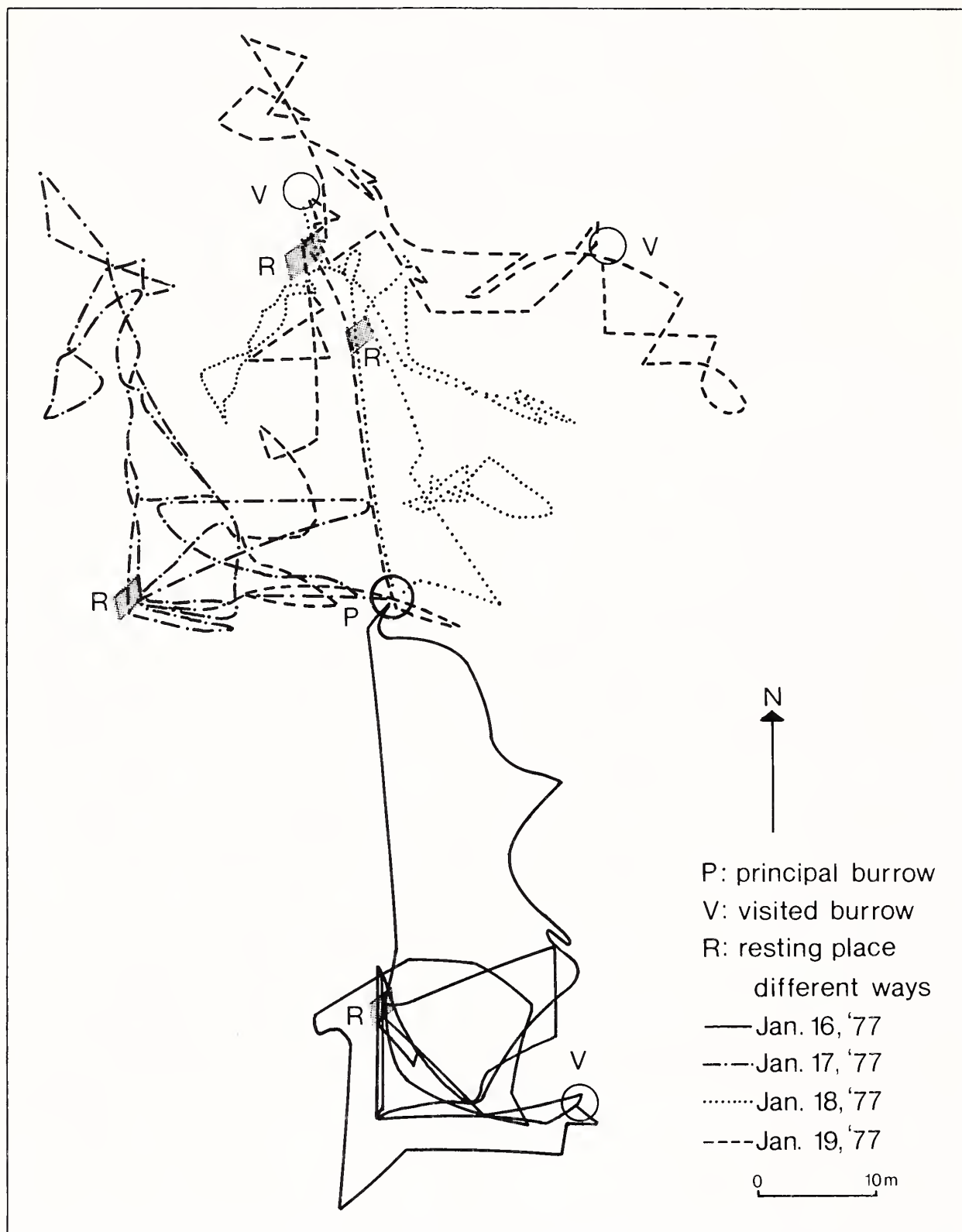


Fig. 2.—Movements of an individual male *Hybomys* monitored by the radio-tracking technique. Daily movements are recorded for 4 days in January 1977.

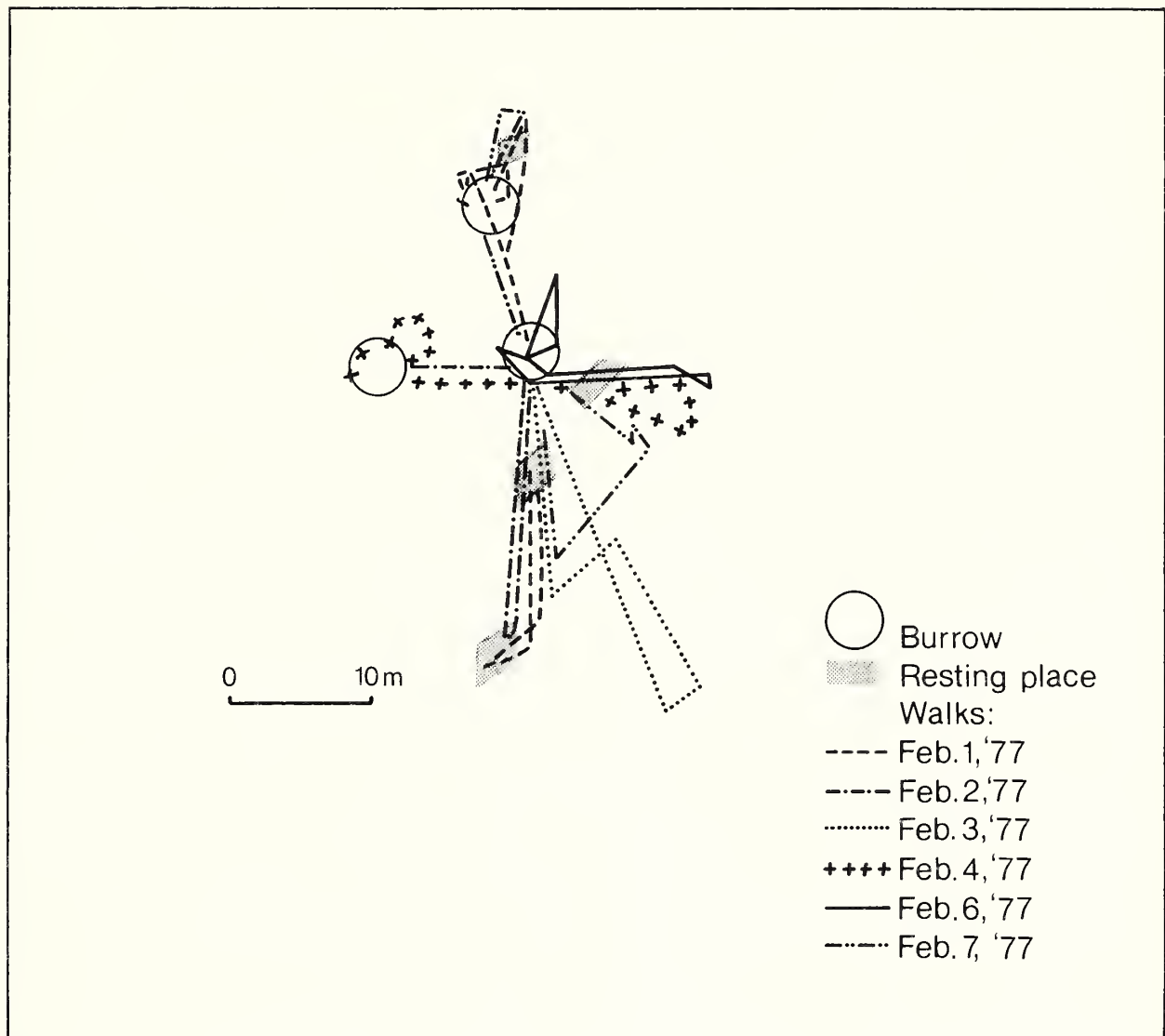


Fig. 3.—Movements of an individual female *Hybomys* monitored over a 6-day period in February 1977. Numerous short movements around the burrows are not indicated.

months chooses to go with a neighboring male. However, it can be seen that the coexistence of the two sexes is not the rule. The individuals do not sleep in the same burrow. Surely the overlapping of the home ranges favors mating in the breeding season.

Hybomys Activity in the Forest

All the activity of *Hybomys* outside of the burrow is diurnal. Males and females do not have the same type of activity.

Case of males.—The activity timetable of males is rather regular for an individual but it varies from

one individual to another. Thus an early-rising male may leave its burrow near 7:20 A.M., whereas another may wait until 8:30 to 8:50 A.M. The individual will run quickly a distance of 20 to 30 m to reach a part of its home range that it will be exploring carefully during the next several hours. It follows a different path each day and some of them do not visit the same part of their home range on two consecutive days (see Fig. 2).

In the morning, movement is done at top speed, but in the afternoon the animals are not so swift. During the day, we have observed short periods of decrease in movement, but they are not a true rest

period, because the animal feeds or performs its toilet.

Besides these short periods of non-movement, there are two resting periods, one or two h long. The first is in the middle of the morning and the second in the course of the afternoon (for instance between 9:00 and 10:00 A.M. and between 4:30 and 5:30 P.M.). Males take their rest in their principal burrow (that is to say in the burrow where the animal spends most of its nights) or in some special areas that *Hybomys* like very much (for example, piles of twigs, dead branches, underpart of a blown down trunk, or old "termite houses" with many holes). Sometimes several species of rodents share the same "termiterium." *Hybomys* returns to these places many times in the course of its walks.

Each day, a male covers a distance of about 500 m. This distance has been evaluated by summing up all the recorded movements. I have not been able to take into account the numerous sporadic movements and small bolts that the animal does in quest of food; such activity is not perceptible with my method of telemetry.

The mean speed of a male *Hybomys* varies between 110 cm/min in the morning, to 80–90 cm/min in the afternoon, but it can reach a higher speed. For instance, an animal released at dusk at the place of its capture tries only to return to its resting place and it does that at a speed of 720 cm/min. It does not run directly to its burrow, but describes a large circle, as if trying to get its bearing, and it does not come into its hole without turning around first.

A male usually spends the nights in the same burrow. It regularly visits three or four other burrows in which it occasionally sleeps, and sometimes visits the burrow of a female, which may live in an overlapping home range.

The last return to the principal burrow takes place between 6:00 P.M. and 6:05 P.M. or between 5:45 and 5:50 P.M., according to the individuals in-

involved. If the males don't begin their activity at the dawn, they cease their activity at full dark in the forest.

Female activity.—Females are not as active as males. They move only short distances; they circle their burrows, entering into them often, even if there are no young in the nest. They repeat this frequently and do not go further than 50 m from their burrows. Thus, females are sedentary, but, quite curiously, they have several burrows and can spend a night in each of them; those burrows are about 10 m apart (Fig. 3).

In the course of a day, a female can spend long periods out of its burrow. It remains motionless under dead leaves, and returns to the same places for consecutive days between 10:00 A.M. and 4:00 P.M. At times, it takes a long rest in its burrow, for 40 min to 2 h between 10:00 A.M. and 4:00 P.M.

Female activity begins between 7:45 and 8:30 A.M. and the activity ceases between 5:00 and 6:00 P.M.

The time of activity of a female and of a male are not very different, but the females are not so regular. The most striking difference between male and female activity concerns the intensity of this activity and the length of the movement. It appears that females are not so strongly attached to their home range as males, since even as adults, they can leave one home range for another. A female, which lived in January on a part of the home range of a male, was caught in April, and watched during 3 weeks by the radio-tracking technique on another area. This latter was situated 70 m from the first area, overlapping the home range of another male slightly (see Fig. 1). In addition, females are not so "home-loving" since they scarcely spend two consecutive nights in the same burrow when they have no young.

This paper was communicated by Francis Petter.

SEASONAL POPULATION CHANGES IN RODENTS IN THE KENYA RIFT VALLEY

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ABSTRACT

Live trapping of small rodents was undertaken on three grids each of 81 traps in grassland and scrub vegetation in the middle of the wet and dry seasons in Nakuru National Park, Kenya. Snap trapping was carried out concurrently. The most abundant species was *Arvicanthis niloticus*; *Praomys natalensis*, *Lemniscomys striatus*, *Otomys angoniensis*, and *Rhabdomys pumilio* were obtained in moderate number. There were relatively greater changes in densities in the grassland than in the scrub at the two trapping occasions; densities were invariably highest in the

dry season. Reproduction was maximal in the wet season and had terminated by the dry season. Populations of *Arvicanthis* contained animals of all ages at both periods, whereas *Praomys* had a much broader age spread in the wet than the dry season when few older animals were present. The scrub vegetation apparently forms population reservoirs at adverse times of the year when it appears that the grassland is unable to provide suitable conditions.

INTRODUCTION

In recent years several studies have been undertaken on the ecology of small rodents in the grasslands of East Africa (Delany 1964, Delany and Neal, 1969; Neal, 1970; Cheeseman, 1975; Taylor and Green, 1976). With the exception of Taylor and Green's (1976) work, which was undertaken in the same region as the present study, the remaining research has been carried out in western Uganda. These latter studies examined times of breeding, population dynamics, and other aspects of the ecology of animals in areas where there are typically two discrete rainy seasons. In Uganda it was found that the breeding of most species of small rodents commenced soon after the onset of the wet season and terminated shortly after it ended (Delany and Neal, 1969). Inevitably, these breeding patterns exerted their influence on population dynamics throughout the year (Cheeseman, 1975).

In their study at Nakuru and Kitale in Kenya, Taylor and Green (1976) examined the relations between reproduction, diet, and climate. They demonstrated that the seasonal effects of rainfall on the vegetation brought about variations in the quality and quantity of available food for rodents, some of

which could be associated with the regulation of breeding. This valuable work was based upon animals obtained by snap trapping and did not provide detailed information on seasonal changes in population densities and structure. The present study supplemented and extended the work of Taylor and Green (1976) by providing information on these aspects of small rodent ecology in a typically grassland locality having a single protracted rainy season. This rainfall pattern prevails in many parts of the Kenya Rift Valley. Here the rains build up to a peak in March and April from the dry season in December and January. Typically, they continue into November without a break (Fig. 1). This attenuated wet season is not commonly found in the seasonal tropics where the rains usually last for appreciably shorter periods. The field work in this study was undertaken at Baharini Wildlife Sanctuary of Nakuru National Park on the northern shores of Lake Nakuru, Kenya, during July, August, and December 1974 and January 1975. These periods coincided with the middle of the wet and dry seasons.

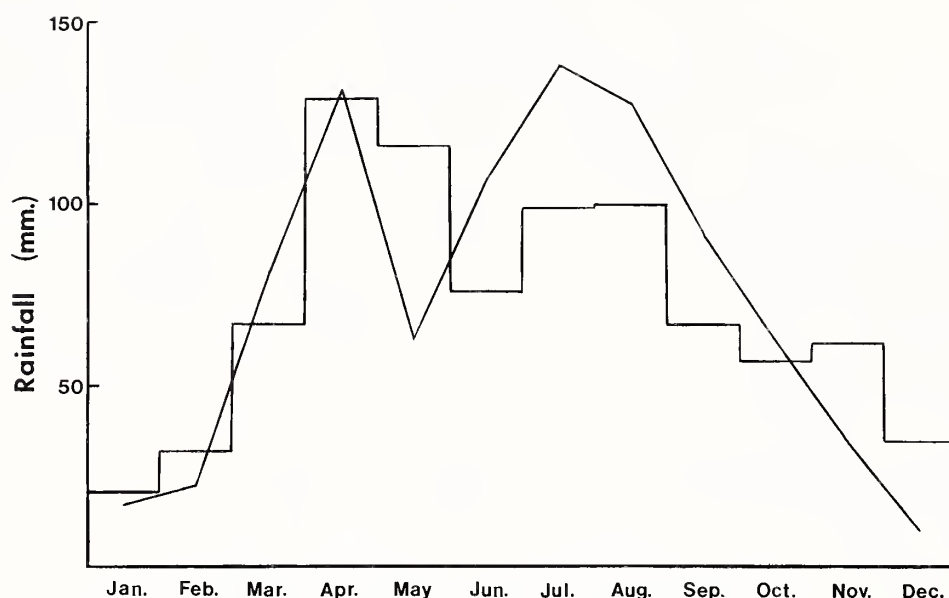


Fig. 1.—Rainfall figures at Nakuru Railway Station. The histograms represent the mean figures from 1904 to 1970 and the continuous line 1974 figures (source: East African Meteorological Department).

STUDY AREA

The field research was undertaken in a relatively small area of grassland with occasional scrub to the north of Lake Nakuru and never more than 3 km from the lake shore. Hereabouts the lake is fringed by a narrow strip of olive bark acacia (*Acacia xanthophloea* Benth.) woodland with an understory of shrubs, herbs, and grasses including *Setaria pallidifusca* (Schumacher) C. E. Hubb, *Erlangea cordifolia* (Benth. ex Oliv.), *Tagetes minuta* L., *Abutilon mauritianum* (Jacq.) Medic., and *Solanum* sp. Beyond this woodland lies an extensive and level area of grassland, which to the east rises to a stony hillside covered by small *Acacia* trees. Here extensive rock outcrops result in a poor covering of ground vegetation.

Between the lakeside woods and the hillside, the extensive grasslands were interspersed with very small patches of scrub, and the occasional tree or small clump of trees. It was within an area approximately 3 km square of this grassland and scrub that the research was concentrated. This was at an altitude of 1,870 to 1,950 m above sea level. Within this area live trapping was undertaken in five grids and snap trapping over the area as a whole within its typical vegetation types. As considerable reference is subsequently made to the grid trappings, their vegetation is given in some detail.

Grids 1 and 2 were placed in an extensive and

typical area of grassland. Here in July much of the vegetation was 1 m or more tall and consisted mainly of *Hyparrhenia hirta* (L.) Stapf., *Themeda triandra* Forsk. and *Chloris gayana* Kunth. *Sporobolus pyramidalis* Beauv., *Setaria pallidifusca* (Schumacher) C. E. Hubb, *Aristida adoensis* Hochst., and *Harpachne schimperii* A. Rich. were also present. The area was interspersed with a few small *Acacia* trees, the occasional compact bush of *Lippia javanica* (Burm. f.) Spreng, small woody *Hibiscus aponeurus* Sprague and Hutch., and scattered *Solanum* plants up to approximately 60 cm tall. There were numerous small herbs adding to the thickness of the ground cover. Over most of these grids the grass and herbage formed a dense cover although there were a few small areas of sparsely covered ground. In addition to the rodents obtained in this work, other mammals present included spring hares, *Pedetes capensis* (Forster), mole rats, *Tachyoryctes splendens* (Ruppell), ant bears, *Orycteropus afer* (Pallas), and steinbok, *Rhaphicercus campestris* (Thunberg). A herd of waterbuck, *Kobus ellipsiprymnus* (Ogilby), were occasional visitors.

Grid 3 contained slightly different vegetation to grids 1 and 2. Although there was a good grass cover of *Hyparrhenia*, *Themeda*, *Setaria*, *Aristida*, and *Chloris* on about three quarters of the grid, more herbs and shrubs interspersed with the grasses over

the remainder. These included *Erlangea*, *Lippia*, *Indigofera vohemarensis* Baill., *Leonotis*, and *Tagetes*. There was also a small clump of trees.

The vegetational character of grid 4 and grid 5 was quite different from the preceding three grids. In view of the detailed studies undertaken on them, these two grids had their vegetation mapped. Whereas grids 1 to 3 were within grass-dominated vegetation, 4 and 5 had a much more shrub and bush character. On grid 4 grasses (*Hyparrhenia*, *Themeda*, *Aristida*, *Chloris*) were present but covered little ground. *Lippia* was abundant and dense, attaining a stature of 50 to 150 cm over much of the grid. It was frequently accompanied by dense *Cynodon aethiopicus* Clayton and Harlan. Among the other plants present were *Ocimum suave* Willd., *Alternanthera aspersa*, *Zehneria scabra* (L. f.) Sand., *Bidens pilosa* L., *Rumex usambarensis* (Dammer), *Tagetes*, *Leonotis*, *Solanum*, and *Erlangea*. Over much of this grid the thickness of the vegetation made it difficult to penetrate and necessitated the establishment of narrow footpaths.

Grid 5 was similar to grid 4 in that it had the same shrubby character and contained large amounts of *Lippia*. There was more grass in grid 5 although the shrub-like character was much in evidence. It did not contain as great a variety of herbs and woody plants as grid 4 and was more readily penetrable.

Grids 4 and 5 were located 2 km from the track around the lake along the road to Lanet. They were situated 5 m to the west of this road and almost parallel to it. The two grids had the same compass bearings and were only 21 m apart. Because of their spatial relationship to the road, it was not possible to align them so that they had a continuous base line. Grid 5 was therefore displaced 10 m west of grid 4. These grids covered 40 square m. The vegetation described for these grids was largely confined to the two small patches encompassed by them. They were surrounded by the grassland described for grids 1 and 2.

The vegetation described in these 5 grids is typical of the non-wooded areas to the north of Lake Nakuru. The removal trapping was undertaken in these types of vegetation. Neither cattle grazing nor burning had taken place in the area for some years prior to this study.

In 1974, the rainfall at Nakuru (Fig. 1) was similar to, if not quite the same as, the statistical average pattern. Higher than average rains fell from May to September and the mid wet season trough was earlier than usual. However, April had its typically high rainfall and the total figure for 1974 of 887 mm was only 26 mm more than the mean. It would therefore appear that the figures for 1974 approached the typical situation.

METHODS

Grid trapping was undertaken using 81 (9 by 9) of the larger Sherman live traps. On grids 1 and 3 the spacing was 10 m, on grid 2, 20 m with alternate trap sites of grid 1 forming the central core of this grid, and on grids 4 and 5, 5 m. Traps were examined twice daily in early morning and late afternoon. On capture, each animal was identified to species, weighed, sexed, marked by toe clipping, and the location of the trap in which it was caught recorded. For males it was noted if the testes were descended and for females if they could be recognized as pregnant and/or lactating. They were then released. Traps were set on the grids on the following dates: grid 1—11–14 July 1974, 3–8 January 1975; grid 2—15–17 July 1974; grid 3—1–3 August 1974; grid 4—5–11 August 1974, 28 December 1974 to 2 January 1975; grid 5—18–24 August 1974, 20–25 December 1974. To ascertain occupancy immediately peripheral to grid 4 at the August trapping two rows of traps 5 m apart were set along the two sides of this grid that were not bounded by the road or grid 5. They were in grassland and were set from 14 to 16 August 1974. The catch was handled in the same way as other live trappings.

Snap trapping took place concurrently with the live trapping using 40 commercially produced rat traps. They were set in trap lines and moved at irregular intervals largely in response to their success. The animals caught by these traps provided more detailed information on reproduction and relative age than the live caught animals. They had the standard external measurements taken and were weighed. Reproductive and development conditions were recorded. These included the condition of the uterus (active, distended, inactive, undeveloped, number of placental scars), number of embryos, weight of reproductive tract of pregnant females, lactation, descent and size of testes, and juvenile pelage. Relative ageing was undertaken using seven categories of dental attrition in the upper molar row. The categories, erected for this study, ranged from the incompletely erupted row of Class I to the row displaying considerable dentine exposure in Class VII. A similar method was used by Delany (1971) and Cheeseman (1975). Throughout all the trappings a banana-flour paste was used as bait.

RESULTS

Numbers Caught

In grids 1, 4, and 5 (Table 1), there was a considerable increase in rodent numbers between July and

August and December and January. These increases ranged from double to fifty-fold in the case of grid 1. *Arvicanthis* and *Praomys* comprised just

Table 1.—Numbers of rodents caught on grids 1, 4 and 5.

Species	Grid 1				Grid 4				Grid 5			
	July		January		August		December		August		December	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>Arvicanthis niloticus</i> (Desmarest)	0	0	20	20	4	13	25	25	22	13	31	25
<i>Dendromus melanotis</i> Smith	0	0	0	1	0	0	0	0	0	0	0	0
<i>Lemniscomys striatus</i> (L.)	0	0	0	0	3	0	4	8	0	0	0	0
<i>Otomys angoniensis</i> Wroughton	0	0	0	1	2	1	0	1	2	0	3	2
<i>Praomys natalensis</i> (Smith)	0	1	1	0	13	7	16	7	3	3	7	6
<i>Rhabdomys pumilio</i> (Sparman)	0	0	6	3	0	0	7	7	0	0	9	2
Total	1		52		43		100		43		85	

over 80% of the catch. The patterns of increase from mid-wet to mid-dry season were not the same for each grid. On all three grids there was a considerable increase in the numbers of *Arvicanthis* and *Rhabdomys* while on grid 4 *Lemniscomys* and grid 5 *Praomys* also showed appreciable increases. On grid 4, three *Arvicanthis*, three *Praomys*, and one *Rhabdomys* caught in August were recaptured in December; on grid 5 the comparable figures were six *Arvicanthis* and one *Praomys*. These figures suggest either a low survival or appreciable immigration from the grids. At each trapping period there were a small number of animals caught on both grids. In August there were four *Arvicanthis* and in December-January seven *Praomys*. This indication of relatively small home ranges obtains support from catches from the two peripheral lines of traps by grid 4 in August. One *Arvicanthis*, five *Praomys*, and one *Otomys* were trapped. Of these, only one *Praomys* had been caught on the grid in one of the outer rows of traps.

The catches on grids 2 and 3 were small and they were not worked in the dry season. No animals were taken on grid 2 and one *Mus minutoides* Smith

and two *Lemniscomys striatus* were obtained from grid 3.

The animals caught by snap trapping are given in Table 2. Similar trends are witnessed in species abundance as were found for the live trapping with *Arvicanthis* and *Praomys* most frequently caught. Two additional species (*Lophuromys* and *Aethomys*) were obtained by these trappings.

Population Densities

Fleming's (1971) direct enumeration method has been used to obtain population densities. This is likely to be a conservative estimate as it assumes that all the animals inhabiting the grid are caught in the course of trapping. To provide an estimate of the catchment area of the grid a strip with a width equivalent to the average distance (Av.D.) between successive captures is added to the trapped area. This estimate varies from species to species, from grid to grid and from one time to another. The summary of calculable estimates is given in Table 3. Av.D. could not be obtained for those species where few recaptures were made. The available data suggest that in grids 4 and 5, when allowance

Table 2.—Rodents obtained by snap trapping.

Species	July/August		December/January		Total
	♂	♀	♂	♀	
<i>Aethomys chrysophilus</i> de Winton	0	0	0	1	1
<i>Arvicanthis niloticus</i>	16	12	26	26	80
<i>Dendromus melanotis</i>	0	0	0	1	1
<i>Lemniscomys striatus</i>	3	0	1	1	5
<i>Lophuromys flavopunctatus</i> Thomas	0	0	1	1	2
<i>Otomys angoniensis</i>	5	1	3	2	11
<i>Praomys natalensis</i>	12	16	11	9	48
<i>Rhabdomys pumilio</i>	0	1	7	4	12

Table 3.—Estimates of population densities.

Grid and species	July/August			December/January		
	Av.D. (m)*	Sample size	Nos./ha	Av.D. (m)*	Sample size	Nos./ha
Grid 1						
<i>Arvicanthis niloticus</i>	—	0	0.0	21.16	19	26.8
<i>Rhabdomys pumilio</i>	—	0	0.0	20.60	8	6.1
Total			0.0			32.9
Grid 4						
<i>Arvicanthis niloticus</i>	14.08	19	36.7	10.02	83	116.0
<i>Lemniscomys striatus</i>	?	?	?	12.38	18	28.8
<i>Praomys natalensis</i>	12.35	34	48.0	14.17	26	48.3
Total			84.7			193.1
Grid 5						
<i>Arvicanthis niloticus</i>	13.67	55	77.0	10.88	93	145.6
<i>Praomys natalensis</i>	24.50	5	7.8	11.58	28	32.5
<i>Rhabdomys pumilio</i>	?	?	?	8.50	12	34.1
Total			84.8			212.2

* Av.D. = Average distance between successive recaptures.

is made for underrepresented species, densities range from 100 to over 200 rodents per ha. These densities are probably minimal as there was little evidence of animals ranging far beyond the boundaries of the grids so that the added strip is probably a maximal addition to the area. It is also possible that not all the animals present were trapped.

Grid 1 demonstrates an increase from about one animal per ha in July to a figure approaching 40 in January. On this grid, with twice the interval between traps as on grids 4 and 5, the number of recaptures of *Arvicanthis* is markedly reduced. For example, 35 animals were recaptured 55 times on grid 5 in August, whereas 40 animals were recaptured 19 times on grid 1 in January. This could imply that *Arvicanthis* by having a small home range encountered traps less frequently on grid 1 in which case the figures on Av.D. may emphasize the more extended movements and so provide a relatively high estimate. Should this be so, the density here will be underestimated.

Population Structure

The population structure has been examined for *Arvicanthis* and *Praomys* from body weights and dental attrition. In *Arvicanthis* (Fig. 2) the weight range of 11 to 130 g is represented in both trapping periods. Unlike the dry season data, the July and August figures display a bimodality. The smaller left-hand peak possibly represents animals recruit-

ed into the population in the current wet season. Although this bimodality is not evident in the tooth wear data, they do suggest a high recruitment of young animals into the population at this time. Males attain heavier weights than the females. The female appearing in the 111–120 g category in August was pregnant, which added 35 g to her weight. At both collecting periods recruitment had recently been taking place. Furthermore, there were similar proportions of older animals in the two samples.

In *Praomys* (Fig. 3), there is a wider range of weights and tooth wear categories in the wet season sample as this contains a considerable element of animals weighing less than 25 g. The dry season sample has a much more compact structure as indicated by both body weight and tooth wear. By December there is apparently little recruitment and the older group of animals present in August has been lost from the population. This group will presumably be replaced as the main cohort increases in size over the following 6 months.

These differences between *Arvicanthis* and *Praomys* may be partly explained by their different growth and development rates. Taylor and Green (1976) report that in the laboratory *Arvicanthis* attains a weight of 45 g in 3.5 to 4 weeks, whereas *Praomys* takes 6 weeks to attain 25 g. *Arvicanthis* can reproduce at 4 weeks, but *Praomys* takes 3.5 months to reach breeding condition (Johnston and Oliffe, 1954).

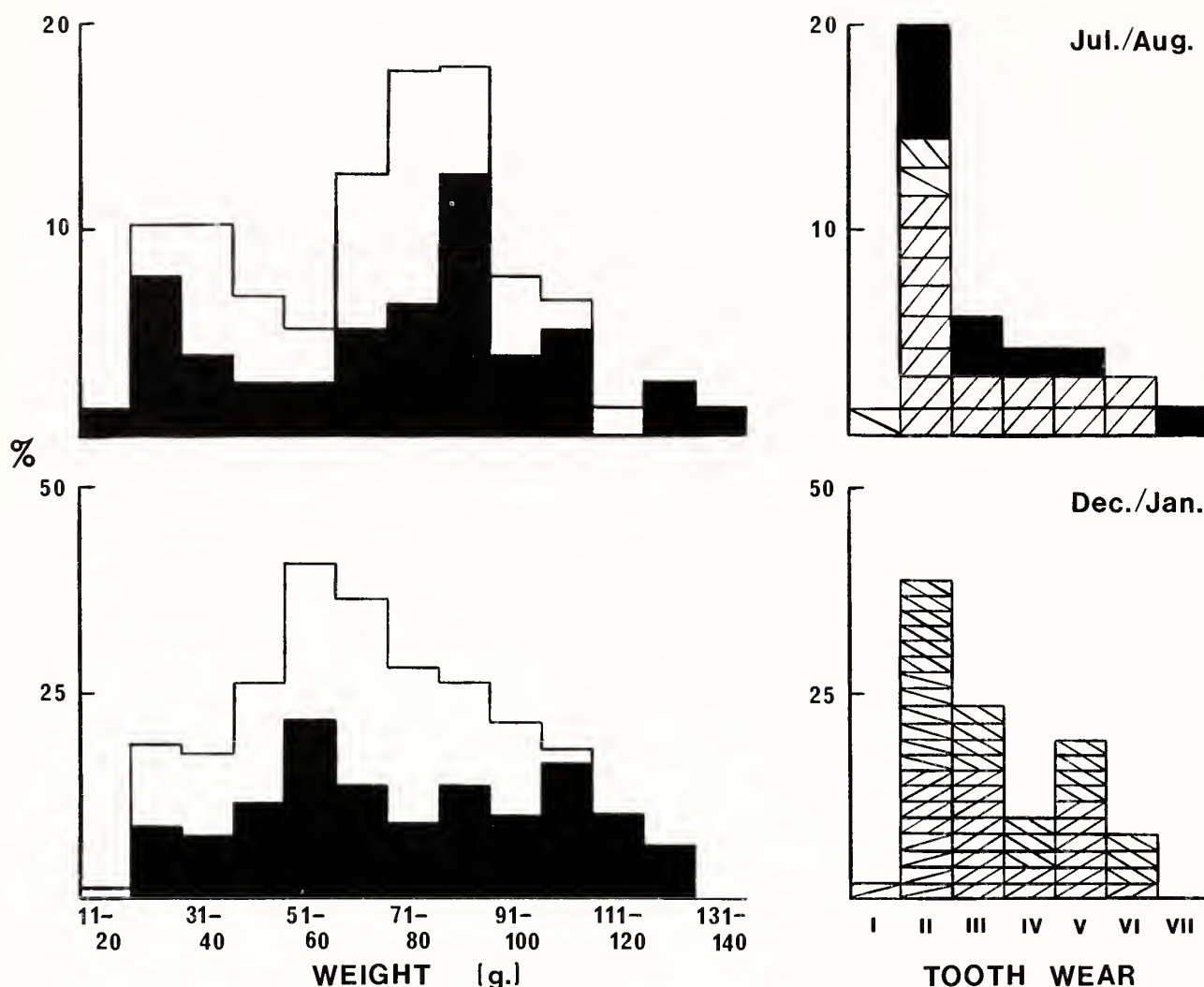


Fig. 2.—Weight and tooth wear distributions and reproductive condition of *Arvicanthis niloticus* in the middle of the wet (July–August) and dry (December–January) seasons. The data on weights include all 276 live and snap-trapped animals. Males and females are represented by solid and open blocks, respectively. The tooth wear histograms are based exclusively on 80 snap-trapped animals. Pregnant females are indicated in solid black, mature females by two lines falling to the right, immature females by one line falling to right, mature males by two lines rising to the right, and immature males by one line rising to the right.

Reproduction

The most comprehensive reproductive data were obtained on *Arvicanthis* and *Praomys* (Figs. 2 and 3). For the remaining species data were scant. Two mature female *Rhabdomys* and *Otomys* were obtained in the wet season; the latter was pregnant with four embryos and lactating. In the dry season two adult female *Rhabdomys* and one *Lemniscomys* were not in breeding condition, whereas the only female *Otomys* and *Lophuromys* collected were both pregnant with three embryos each.

In both *Arvicanthis* and *Praomys* breeding was intense in the middle of the wet season with almost

all mature animals reproductively active. The number of embryos in eight pregnant *Arvicanthis* females were five, six, seven, seven, seven, seven, nine, and nine. The only mature female that was not pregnant was lactating and contained 14 placental scars. This animal could have already produced two litters. Although the identification of scars in pregnant animals is difficult, other indicators of the time of the onset of breeding are available. These include the relative age of embryos, lactation, and the recruitment of immatures. Four of the pregnant *Arvicanthis* were in early pregnancy with reproductive tracts weighing less than 2 g. Two of these were

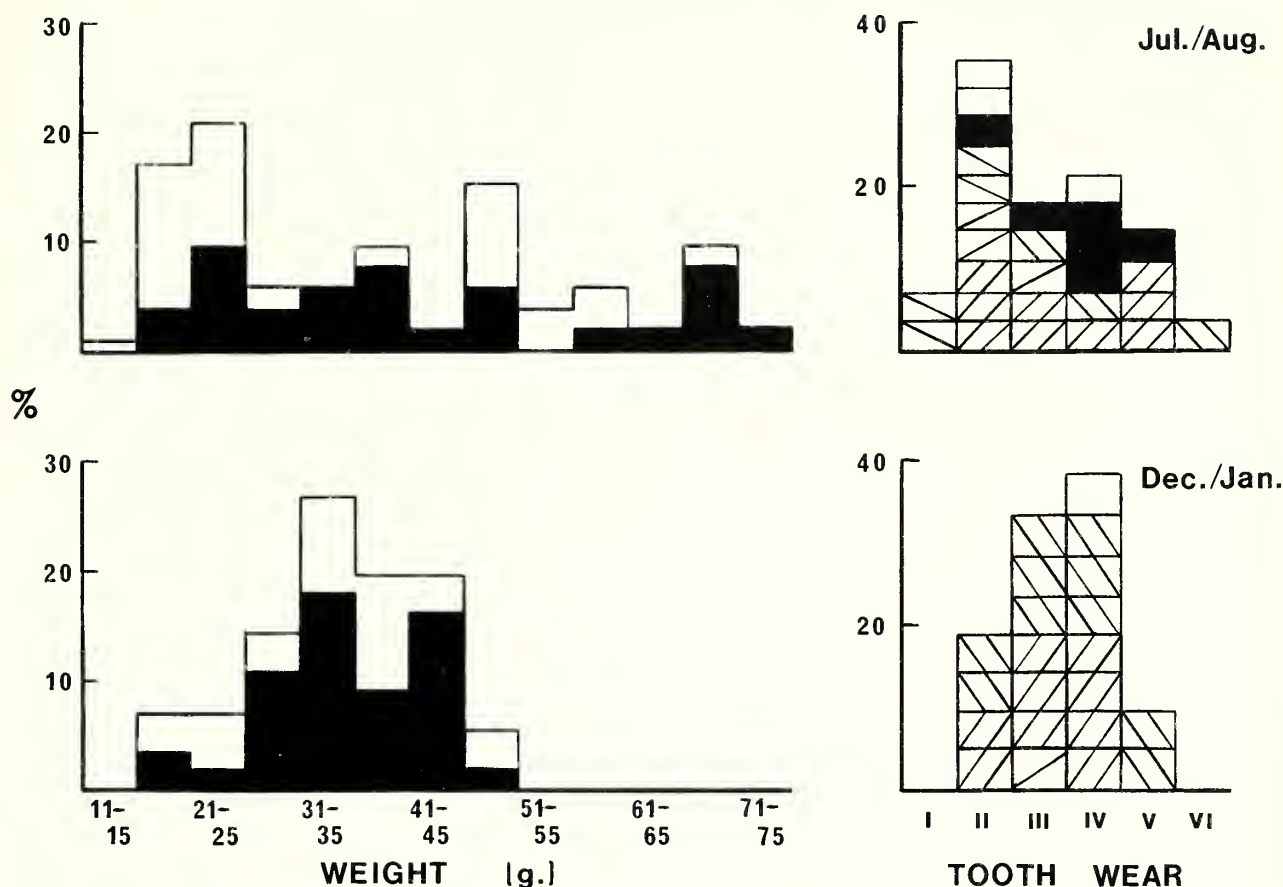


Fig. 3.—Weight and tooth wear distributions and reproductive condition of *Praomys natalensis* in the middle of the wet (July–August) and dry (December–January) seasons. Legend as for Fig. 2. The open blocks in the tooth wear histograms are of unsexed animals. The data on weights and tooth wear are based upon 109 and 49 animals, respectively.

lactating and were probably suckling litters in the nest. In contrast, one female was near full term with her nine embryos each having a mean weight of 3.2 g. On this evidence it appears that breeding must have been under way for approaching two months. The date of termination of breeding is more difficult to ascertain. By early January 11 of 52 animals taken were immature and could have been conceived six to eight weeks earlier. All adult females contained placental scars. These clustered around a mode of four (four, four, four, five, nine, 12, 12, 12, 15, 16) which could suggest an average litter approximating to this figure. This obtains support when only the larger and more prominent scars are included in the counts. The figures for these 10 animals are then five with four scars, three with five, one with six, and one with seven, a mean of 4.8. If these animals were latterly producing litters of this size, they were much smaller than the mean of 7.1 recorded earlier in the year.

Praomys had been reproducing for some time prior to July with 36% of the population comprised of immature, young animals. As with *Arvicanthis*, the impregnated females ranged from the recently conceived to near full term. Embryo numbers for five pregnant females were seven, seven, nine, nine, and nine. By late December, *Praomys* appeared to be well into reproductive anoestrous. Scars were only seen in two of the adult females; they numbered 10 in the one in which they could be counted. Only 5% of this sample were immature, compared to 21% in *Arvicanthis*. These differences are supported by the demographic data. It is of note that reproduction was taking place in young animals with low tooth wear values.

Range Length

As the number of recaptures (Table 4) on the grids were relatively small for the calculation of meaningful home range sizes it was considered that

Table 4.—Adjusted range lengths.

Species	Grid	Date	No. of captures										Mean range length (m)	Range (m)
			2	3	4	5	6	7	8	9	10	Total		
<i>Arvicanthis niloticus</i>	4	Aug	3	1	4	—	—	—	1	—	—	9†	26.50	10–56
<i>Arvicanthis niloticus</i>	4	Dec	12	10	9	2	2	1	—	—	—	36	19.71	5–40.5
<i>Arvicanthis niloticus</i>	5	Aug	—	4	—	3	1	—	1	1	1	11	29.22	12–40.5
<i>Arvicanthis niloticus</i>	5	Dec	11	8	6	7	1	2	—	—	—	35	21.61	10–47.5
<i>Arvicanthis niloticus</i>	1	Jan	12	2	1	—	—	—	—	—	—	15	31.10	10–73.5
<i>Praomys natalensis</i>	4	Aug	3	3	2	—	1	1	1	—	1	12	25.95	5–47
<i>Praomys natalensis</i>	4	Dec	5	4	3	4	1	—	—	—	—	17*	31.41	10–82
<i>Praomys natalensis</i>	5	Aug	1	2	—	—	—	—	—	—	—	3	34.50	21–52
<i>Praomys natalensis</i>	5	Dec	—	—	2	3	—	—	—	—	—	5	27.60	19–50

† Three of these animals were also caught on the adjacent grid 5.

* Seven of these animals were also caught on the adjacent grid 4.

a useful alternative would be the estimation of range length. This involves calculating the distance between the two furthest points of capture and adjusting this figure by the addition of the distance between traps. The mean range length figures for *Arvicanthis* on grids 4 and 5 are smaller in December. The high figure on grid 4 in August was influenced by three animals being occasionally found on grid 5. On grids 4 and 5 in December only three and four animals, respectively, had ranges of more than 30 m. During this period no animal was caught on both grids. These combined data suggest smaller home ranges in December when densities are higher.

The *Praomys* samples for grid 5 are particularly small. The data from grid 4 suggest a small increase in range length in a population showing little change in density from August to December. The increased range length is influenced by the considerable movement between the two grids by this species in December. *Praomys* may be more wide roaming

than *Arvicanthis* as during August an animal marked on grid 4 was snap trapped 100 m from it. Cheeseman (1975) found this species had a small compact home range in *Imperata* grassland and a mean adjusted range length of 75 m.

Distribution on the Grids

With such high densities of rodents populating grids 4 and 5, it is particularly relevant to consider how resources within them might be partitioned. This can be indirectly assessed by the examination of distribution within the grids, assuming that the capture of an animal within a trap is an indication of the animal favoring the environment in the trap's immediate vicinity. This information can be obtained by analyzing the success of each trap and noting its location in relation to the vegetation. On grid 5 the vegetation could be subdivided into two intergrading categories. *Lippia* was present over all the grid, although in some places it was more dominant than others where there was a greater amount of grass. There were then *Lippia* and *Lippia*-grass habitats. It was found that 30 traps were located in the former and 51 in the latter. The total number of catches by traps in these two broad divisions are summarized in Table 5. The results show that in August *Arvicanthis* favored the bushy *Lippia* with more than twice as many catches being made in it than in more grass encroached areas. By December, when the population had almost doubled, the number of catches in the *Lippia* had not increased greatly, whereas elsewhere the increase had been dramatic. As these *Lippia*-grass areas occupied the

Table 5.—Catches of rodents in the main vegetation types of grid 5. Figures are expressed as number of catches per trap.

Species	Date	Grass and	
		<i>Lippia</i>	<i>Lippia</i>
<i>Arvicanthis niloticus</i>	Aug	1.70	0.65
<i>Arvicanthis niloticus</i>	Dec	1.87	1.47
<i>Praomys natalensis</i>	Aug	0.07	0.18
<i>Praomys natalensis</i>	Dec	0.50	0.43
<i>Rhabdomys pumilio</i>	Dec	0.07	0.33

Table 6.—Trap success on grid 4.

Species	Date	No. of captures in the same trap								Total animals
		0	1	2	3	4	5	6	7	
<i>Arvicanthis niloticus</i>	Aug	65	9	4	1	1	1	—	—	17
<i>Arvicanthis niloticus</i>	Dec	29	16	15	14	4	1	1	1	50
<i>Praomys natalensis</i>	Aug	48	26	2	4	1	—	—	—	20
<i>Praomys natalensis</i>	Dec	49	21	9	2	—	—	—	—	23
<i>Rhabdomys pumilio</i>	Dec	73	4	2	2	—	—	—	—	14
<i>Lemniscomys striatus</i>	Dec	63	12	2	4	—	—	—	—	12

In August 11 traps caught two species: *Arvicanthis/Praomys*, 8; *Praomys/Otomys*, 2; *Praomys/Lemniscomys*, 1.

In December 32 traps caught two or three species: *Arvicanthis/Praomys*, 9; *Arvicanthis/Lemniscomys*, 5; *Arvicanthis/Praomys/Lemniscomys*, 7; *Arvicanthis/Praomys/Otomys*, 1; *Arvicanthis/Praomys/Rhabdomys*, 1; *Praomys/Rhabdomys*, 3; *Praomys/Lemniscomys*, 4; *Rhabdomys/Lemniscomys*, 1.

larger portion of the grid they would be able to spatially accommodate much of the increased population. *Praomys* was caught less frequently in the *Lippia* when in low numbers, but by December when numbers had increased appreciably it was caught almost equally in both vegetation types. *Rhabdomys* was demonstrably more common in the *Lippia*-grass vegetation.

The vegetation on grid 4 formed a complex mosaic, which did not readily permit subdivision into broad categories. The stature of the bush varied within the grid as did its composition. Furthermore, there were grassy patches but these were very small (a few square m) and merged imperceptibly with much of the *Lippia*-dominated vegetation. The grassland along two sides of the grid hardly encroached upon it with the distinction between it and the scrub and bush being quite sharp. In view of this vegetational complexity, the data for this grid was analyzed rather differently to that for grid 5. Table 6 records the catches in each trap. In August, 65 traps made no catch of *Arvicanthis*, nine made one catch, four made two catches, and so forth. For this species only 16 traps were visited and most of these were clustered in one corner of the grid close to a warren. By December, with larger numbers present, 52 traps were visited. The 16 traps catching animals in August made 29 captures; the same traps made 26 captures in December. Thus, as with grid 5, there was a greater utilization of the grid with higher numbers.

Praomys numbers did not change markedly over the 4-month interval between the trappings and at both times this species was widely dispersed, favoring no particular sector of the grid. The 33 traps making all the catches in August obtained 14 of the 45 December catches. The December *Rhabdomys* catches were interesting. They were all made in the two outermost rows of traps along the two sides of the grid bounding the grassland. Most *Lemniscomys* catches were made in the half of the grid remote from the track but the distribution of this species apart from its widespread appearance (three traps in August, 13 in December) is difficult to interpret.

With the increase in numbers of rodents on grid 4 the number of traps catching more than one species almost trebled. By December nearly two fifths of the traps caught animals belonging to two or more species (Table 6). There were eight species combinations caught in single traps with no firm indication of any one species excluding another from a particular location. Whatever the ecological requirements may be of individual species there can be little doubt that on this grid several species must live in close juxtaposition. Furthermore, there is the possibility of appreciable intraspecific interaction when animals occur at these densities. From both grids it is suggested that *Arvicanthis* occupies core areas from which it spreads and that these situations do not increase their densities as breeding takes place.

DISCUSSION

There are several important findings from this exploratory study, which involved three months intensive field work. One of the most striking features

is the almost complete absence of small rodents from the swards of open grassland in the middle of the wet season and their relative frequency during

the dry season. Not only was this true of the grid trappings. Such removal trappings as were undertaken in grassland in July and August returned negligible catches and it was only if there were herbs, weeds, and some low bush present that trapping improved. This situation raises several relevant issues. The colonization of grassland must have been rapid over extensive areas. If the 1974 and 1975 conditions were typical, and there was no reason for believing they were not, a decline in numbers could be anticipated in the grassland between January and July 1975. That the events of 1974 represented a single and permanent colonization could only be considered possible if there were some special circumstances, such as fire earlier in the year, or a permanent change in ecological conditions, such as an alteration in the grazing regime of cattle. The authors were assured that neither of these occurrences nor any other observable change in ecological conditions had taken place in the previous few years. This being the case, it appears that these small rodents have permanent localized reservoirs of high density populations which, with the onset of breeding, result in a rapid spread and temporary colonization. When first trapped in July 1974, the grasslands appeared most suitable rodent habitats. There was good cover, a diversity of plant species, and a substratum suitable for the construction of burrows. This was well into the wet season and it can only be assumed that at the end of the dry season and early into the rains, the habitat becomes much less hospitable as the grasses die back.

The dry season density of 30 to 40 rodents/ha in the grassland is of the same order of magnitude as the 13 to 64 animals/ha Cheeseman (1975) found in grassland in western Uganda, which he trapped monthly over a period of 19 months. Here populations never approached the low levels obtained at Nakuru. Misonne (1963) estimated there were 65 rodents/ha in *Hyparrhenia* grassland in Zaire, whereas Bellier (1967) found 22 rodents/ha in savanna in the Ivory Coast. The bush-scrub populations of 100 to 200+ animals/ha obtained in this study were higher than all these grassland figures. Work elsewhere in Africa in mixed and arable vegetation indicate that high densities can be obtained. In a crude estimate of numbers in a small, abandoned cultivated plot near Kampala, Delany and Kansimeruhanga (1970) recorded a density of 160 rodents/ha, whereas in eastern Zaire Dieterlen (1967) obtained 454 rodents/ha in an area of grass, bush, and scrub adjacent to cultivated land, which the

rodents also exploited. The particular significance of the Nakuru situation is the localization of these populations into extremely small pockets. Within the whole study area, grids 4 and 5 were the only patches of this type of vegetation that were sufficiently large to accommodate the small grids used. Dense vegetation occurred in the lakeside woodland but here the removal trappings caught few animals. Furthermore, this vegetation was not the same as that in grids 4 and 5.

The spread of rodents from their localized dense pockets must be associated with an increase in number through reproduction and the availability of suitable resources. As far as can be ascertained, it appears that reproduction commenced about May and terminated in October or November. It is probable that it was continuous throughout this period although this cannot be stated with certainty. Taylor and Green (1976) have shown that at Kitale *Arvicanthis* begins breeding 2 to 3 months after the start of the rains and ceases approximately a month after their termination. Here, reproduction is greatly influenced by availability of seeds and/or cereals which usually do not become available until 2 or 3 months after the beginning of the rains. The breeding of *Praomys* was also dependent on seeds and/or cereals and had a similar pattern to *Arvicanthis*.

Continuous breeding over several months and the ability of *Arvicanthis* to reproduce at an early age make for considerable increases in population densities. It is suggested that this results in the spread into and exploitation of previously uninhabited areas while the production of the grass seed crop would facilitate breeding within them. Such a spread occurred on a very small scale in grids 4 and 5. On grid 5 the dispersal was from the bush dominated to the more grassy areas, a phenomenon apparently having general application. It is interesting that *Praomys* did not become established in the grassland and furthermore, the numbers caught in the scrub did not greatly differ between the two trapping seasons. It was less numerous on grid 5 where the interphase with grassland was more obvious than in grid 4, which was more bushy. This apparent avoidance of grassland is unusual as this is a habitat in which this species can be numerous (Cheeseman, 1975). The same is true of *Lemniscomys*, which at Nakuru was not very common. More *Rhabdomys* were caught, although, again, this was nothing like as numerous as *Arvicanthis*. It is difficult to identify the vegetation this species occupies in the adverse season as it appears to be

absent from grassland and avoiding the scrub. It could resort to the more intermediate situation where grasses and denser herbaceous vegetation meet. The whole study needs extension to consider the ecological requirements of individual species. No examination was made of their food, activity, microhabitat requirement, or social interactions with members of their own and other species. The faunal diversity and population densities make the detailed examination of many of these phenomenon particularly attractive.

There is a further aspect of this study that merits brief consideration. Both *Arvicanthis* and *Praomys* are serious agricultural pests in Kenya (Roberts, 1939; Taylor, 1968) and many other localities in tropical and subtropical Africa (Taylor, 1962, 1969). Their occurrence in large numbers in Kenya can be sporadic (Taylor, 1968), although high densities have been associated with protracted wet seasons

and a rich growth of weeds and other vegetation. In contrast, Taylor and Green (1976) reported *Arvicanthis* absent from their study area in agricultural land at Nakuru for a year. Thus, while this species can be very abundant, it is also sensitive to habitat conditions, which account for its temporary disappearance from large areas. At such times it is probably confined to small nuclei with good cover and adequate food supply. The agricultural environment, particularly where there is cultivation, is unstable and is unlikely to afford good permanent habitation for rodents. However, the retention of small habitable nuclei provide potential reservoirs for establishment over larger areas. The removal of small, unused pockets of scrub and bush would do much to prevent infiltration into cultivated crops. The same could well apply to badly maintained smallholdings where weed growth is permitted and cover for rodents is thereby inadvertently provided.

SUMMARY

The field work was carried out in Nakuru National Park, Kenya, during the middle of the wet (July and August 1974) and dry (December 1974 and January 1975) seasons. The rains occurred from March to November. Trappings were concentrated in mixed, ungrazed grasslands (*Hyparrhenia*, *Themeda*, *Chloris*), and small adjacent areas of scrub in which *Lippia javanica* was an important species.

Most of the live trapping, using 81 large Sherman traps, was in three grids (9 by 9 traps), one in grassland and two in scrub. The latter were 21 m apart and had trap spacings of 5 m; the former had a trap spacing of 10 m. Each grid was trapped in both wet and dry seasons. Snap trapping was undertaken in other parts of the study area.

Arvicanthis niloticus and *Praomys natalensis* were caught most frequently; *Lemniscomys striatus*, *Rhabdomys pumilio*, and *Otomys angoniensis* were obtained in small numbers and *Dendromus*, *Mus minutoides*, *Aethomys*, and *Lophuromys* recorded occasionally. The grassland supported negligible populations in July. During August densities in the scrub approached 100 rodents/ha. By Decem-

ber populations in the latter had increased to 200/ha and in the former 33/ha.

Both wet and dry season populations of *Arvicanthis* contained animals of a wide range of ages. In contrast, the *Praomys* population contained few older animals in December. Reproductive activity was intense in the wet season and virtually nonexistent in the dry season.

At the higher dry season density there was an indication of smaller home ranges in *Arvicanthis*. This species then occupied more extensive areas of the grid than previously. Such dispersal could be a factor accounting for the prevalence of this species in the grassland at this time.

Praomys was frequent in scrub where it was much less numerous than *Arvicanthis*; it was uncommon in grassland. *Rhabdomys* was typically found in this vegetation. The small patches of scrub within the grassland apparently supported reservoir populations of *Arvicanthis*, which, during the reproductive phase, expanded into adjacent grassland.

ACKNOWLEDGMENTS

The authors are grateful to the President's Office, Kenya, the Trustees of Kenya National Parks, and the Baharini Wildlife Sanctuary for permitting this research to be undertaken. For his encouragement and considerable logistic assistance, we would like to thank Mr. J. Hopcraft of Baharini. The wardens of Nakuru National Park readily gave their help and advice. The re-

search was financed through a grant from the Royal Society of London. The East African Herbarium kindly identified the plants. Finally, we would like to thank our wives for their support; one (JR) who patiently waited in United Kingdom and the other (AVD) whose field assistance was greatly appreciated.

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MODERN RODENT FAUNA OF THE LOWER OMO VALLEY, ETHIOPIA

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ABSTRACT

One hundred and seventy rodents, comprising 15 species of nine genera and five families (Sciuridae, Gerbillidae, Cricetomyidae, Muridae, and Gliridae), have been captured in the lower Omo Valley. These represent a good sampling of the modern

rodent population of the several biotopes of the areas—Sahelian savanna, arid zones (paleontological beds), and forested blocks comprising a continuous stratum of large trees and associated bushes and shrubs.

INTRODUCTION

One hundred and seventy rodents, comprising 15 species of nine genera and five families, were captured in the lower Omo Valley in the summer of 1973 during the paleontological expedition organized by Yves Coppens. These represent a good sampling of the modern rodent population of the several biotopes of the areas.

The specific designation of certain species mentioned here cannot always be regarded as definitive, because systematic revisions may be required.

However, their ecological characteristics are well-defined. A future study, based on karyotypes, will permit the systematics of species to be more firmly established.

Animals have been captured in various ways—through excavation of their burrows; by hand at night with the aid of a light; by traps set at burrows or in lines and baited with peanut butter; or by large metal cans sunk half to three-quarters of a m into the ground.

RESULTS

Species List

Sciuridae

Heliosciurus gambianus omensis (Thomas, 1909)*

Xerus rutilus (Cretzschmar, 1826)

Gerbillidae

Tatera nigricauda (Peters, 1878)

Tatera minuscula Osgood, 1936

Taterillus harringtoni (Thomas, 1906)

Gerbillus pulvinatus Rhoads, 1896

Gerbillus pusillus Peters, 1878

Cricetomyidae

Saccostomus mearnsi Heller, 1910

Muridae

Mastomys erythroleucus (Temminck, 1853)

Arvicanthis niloticus (Desmarest, 1822)

Arvicanthis somalicus Thomas, 1902

Acomys percevali Dollman, 1911

Acomys wilsoni Thomas, 1892

Thamnomys dolichurus (Thomas and Wroughton, 1908)**

Gliridae

Graphiurus murinus Desmarest, 1822

*Captured by A. Duff-Mackay (National Museum, Nairobi, in 1967).

**Captured by F. Rhodain and R. Houin.

The presence of at least two other species is indirectly documented. An immense network of burrows, 3 to 5 cm in diameter, situated at a depth of about a meter, occurs on the surface of the Kibish Formation sediments, and may well testify to the presence of a bathyergid mole-rat. Some nests, filled with dry leaves, and unlike those of *Graphiurus* or of *Thamnomys*, were found situated either in hollow limbs or in the empty trunks of certain trees in the gallery forest and could well belong to a species of *Thallomys*, a genus already documented elsewhere in Ethiopia (Petter, 1973).

DISCUSSION

Geographic Distribution

Some species are widely distributed throughout sub-Saharan Africa (*Arvicanthis niloticus*, *Masto-*

mys erythroleucus, *Thamnomys dolichurus*, *Graphiurus murinus*). Others are restricted to eastern Africa (*Xerus rutilus*, *Tatera nigricauda*, *Taterillus*

Table 1.—Number of rodents collected in the five ecological zones of the trapped area in the Omo Valley, Ethiopia. The number of trap-nights is indicated for each zone, but is not significant because some species were collected by digging their burrows or by sunken can-traps.

Species captured	Riverine areas		Arid zones		
	With trees & shrubs	Without trees, with grass & thickets	Slopes	Bottom	Plateau
<i>Xerus rutilus</i>				1	5
<i>Tatera nigricauda</i>	4	11		2	8
<i>Tatera minuscula</i>				2	1
<i>Taterillus harringtoni</i>		1		2	3
<i>Gerbillus pulvinatus</i>					27
<i>Gerbillus pusillus</i>				3	6
<i>Saccostomus mearnsi</i>		9			
<i>Mastomys erythroleucus</i>	2	3			
<i>Arvicanthis niloticus</i>	11	2			
<i>Arvicanthis somalicus</i>		7		5	
<i>Acomys percevali</i>		4	3	16	3
<i>Acomys wilsoni</i>	2	16			9
Total specimens	19	53	3	31	62
Number of trap-nights	640	1,880	290	630	1,711

harringtoni, *Saccostomus mearnsi*, *Arvicanthis somalicus*, *Acomys wilsoni*). Others appear to be more or less endemic and limited in distribution to southern Ethiopia and northern Kenya (*Heliosciurus gambianus omensis*, *Tatera minuscula*, *Gerbillus pulvinatus*, *Gerbillus pusillus*, *Acomys percevali*).

Ecological Aspects

These taxa differ in their biology. Certain species dig burrows and are active nocturnally (*Mastomys erythroleucus*) or diurnally (*Xerus rutilus*). Others are active both day and night and construct nests of dry vegetation at the foot of bushes or in high grasses (*Arvicanthis* spp.). Still others are arboreal and active during the day (*Heliosciurus gambianus omensis*) or the night, and construct nests of dry leaves in hollow limbs (*Graphiurus murinus*) or attach them to bushes or lianas (*Thamnomys dolichurus*). Their nests do not seem to be occupied throughout the year.

Three major habitats may be usefully distinguished (see Table 1). The riverine area has two aspects—with trees and shrubs (including *Trichilia roka*, *Tapura fischeri*, *Ficus sycomorus*, *Celtis integrifolia*, *Ziziphus rubescens*, *Cordia gharuf*) forming a continuous canopy, and with lianas (*Sissus*, *Sabia*) present. This zone appears to have a poor rodent fauna; only *Heliosciurus gambianus omensis*, *Graphiurus murinus*, and *Thamnomys*

dolichurus have been captured. Native villages situated here harbor *Arvicanthis niloticus* and *Mastomys erythroleucus*. There is also the riverine zone, largely without trees, but with grasses and very dense thicket. Here *Mastomys erythroleucus*, *Saccostomus mearnsi*, *Acomys wilsoni*, and *Tatera nigricauda* occur. The soils of this zone are heavy and clay-like and often appear as vertisols. The latter zone is flooded at more or less regular intervals in keeping with the Omo flood regime.

The Shungura Formation exposures may be considered separately and to have three aspects. The slopes of the exposures are comprised of detritus and eroded Plio-Pleistocene sediments. This very arid facies, practically without vegetation, harbors *Acomys percevali*. The cuestas of these exposures, which are covered with tuffs, and the bottoms, which separate them and contain recently eroded sediments, still have a very arid vegetation comprised of open shrubs (*Euphorbias*, *Adenium obesum*, *Cissus rotundifolia*, *Dasysphiera prostrata*, *Commiphora africana*, *Adenia venenata*, *Caralluma russelliana*, *Sesamothamnus brisseanus*, and *Maerua crassifolia*) and rare herbaceous plants (*Indigofera* sp., some Cyperaceae). In these situations *Gerbillus pusillus*, *Taterillus harringtoni*, *Tatera minuscula*, *Arvicanthis somalicus*, and *Xerus rutilus* occur.

Finally, the plateau has several soil types, more or less rich in clay, and these have a considerable

influence on the local composition of the vegetation, generally that of a more or less open shrub or bush savanna (*Acacia paolii*, *A. reficiens*, *A. horrida*, *Grewia tenas*, *Cadaba glandulosa*, *C. gilletti*, *Sciatura hortacantha*, *Serricomopsis pallida*) with herbs (*Blepharis persica*, *Polygala erioptera*, *Ipomea belpharosepala*) as well as numerous grasses (*Aristida*, *Cenchrus*, *Chloris*, *Dactyloctenium*, and others). The plateau rodents are *Xerus rutilus*, *Acomys wilsoni*, and *Arvicanthis somalicus*, which occur everywhere, and *Gerbillus pusillus* and *G. pulvinatus* which occupy areas of lighter, more sandy soil than those where *Taterillus harringtoni* and *Tatera nigricauda* are found.

The distribution of these various rodent species, which utilize the part of the environment which best agrees with their ecological preferences, is further affected by another limiting factor—dryness—which is more or less strongly pronounced according to the year and the season. Except for the gallery forest species, the rodent fauna is rather characteristic of dry, and even arid zones. The low incidence of species in the gallery forest is a result of recurrent dry periods that prevent the occurrence of species that are linked to a permanently moist environment and in addition the occasional flooding of the entire area, thereby restricting immigration by burrowing or purely terrestrial species.

Reproduction

Observations made during the summer of 1973 broadly confirm the conclusions of previous workers (Dieterlen, 1967; Happold, 1966; Poulet, 1972; Hubert, 1977) on the reproduction of tropical rodents in sub-Saharan Africa. Reproduction occurs some weeks after onset of the rainy season. The onset of rains in early July 1973, in the north Shungura area, saw active reproduction of the principal rodent species represented there. In August, 80% of the trapped females were sexually active—either in estrous, gestating, or lactating. Farther south, on

the other hand, in the Kalam area, where rain was lacking, there was no evidence of reproductive activity among those rodent populations.

Taxonomic Comments

The modern rodent fauna of the Lower Omo Valley is typical for this area in Africa, where different types of habitat are represented—Sahelian savanna, arid zones, and forested blocks comprising a continuous stratum of large trees and associated bush and shrubs.

There are two squirrels, one arboreal (*H. g. omensis*, described from this place) and one fossorial (*X. rutilus*). Two species of *Tatera* are present, one widely distributed in eastern Africa (*T. nigricauda*), and a very small one, endemic to this area, *T. minuscula* (which was described by Osgood in 1936 from specimens collected in a nearby area, the Webbi Shebelli in southeastern Ethiopia, and was never officially collected since that time). *Taterillus harringtoni* occurs in all this part of eastern Africa (Robbins, 1975) where it lives together in the Sahelian savanna with two species of gerbils, a medium-sized hairy-footed species, *G. pulvinatus* (Hubert, 1978; Schlitter, personal communication) and a small one with naked sole, subgenus *Hendecapleura*, *Gerbillus pusillus* (Roche, 1976). *Saccostomus mearnsi* is the northern form of this genus, occurring in Ethiopia, Uganda, Kenya, and Tanzania (Hubert, 1978). The *Mastomys* seems to be referable to *Mastomys erythroleucus*, a large species characterized by a light gray belly, a brown-yellowish back, and a karyotype of 38 chromosomes, occurring in western and central Africa (Petter, 1957 and 1978). Two species of *Arvicanthis* are represented—*A. niloticus*, a large species, which is found in wet areas in the savannas over all Africa, and *A. somalicus*, a smaller one with a paler fur, from the arid zones of eastern Africa. The two species of *Acomys* were reported from this area by Matthey (1968).

CONCLUSIONS

It is worth noting that four of the nine rodent genera present in the lower Omo basin are represented each by two species adapted to slightly different habitats. Here is an adaptative evolutionary process of some plasticity frequently found in various animal species. It permits maximum utilization

of the heterogeneity of the environment, in space and in time. This strategy, reflected in more or less marked specialization of different species, adapted to particular conditions, contrasts with that of species substantially less strict in their ecological requirements. However, those latter species are ca-

pable of very rapid occupation of various habitats given some favorable change of a seasonal or other unusual nature.

Thus, the modern rodent fauna of the Lower

Omo basin is rich, reflecting the different habitats present, which is characteristic of the African tropical zones, even the dry zones.

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EVOLUTION OF THE RODENT POPULATION OF A DRY BUSH SAVANNA IN THE SENEGALESE SAHEL FROM 1969 TO 1977

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ABSTRACT

An eight-year study of changes in rodent populations in a Sahel savanna habitat in northern Senegal is presented. Characteristics of population dynamics for the principal species that are most important in allowing repopulation of dry bush savanna

areas include the ability to rapidly attain high population levels after an initial reinvasion. Habitat preference and resource utilization within the dry bush savanna are critical factors to successful increase in population levels and their maintenance.

INTRODUCTION

The evolution of small rodent populations was followed in a Sahel savanna in northern Senegal from 1969 to 1977. Trappings were effected at more or less regular intervals (every one to three months) for the following purposes: to determine the composition of the population and its eventual temporal variations; and to determine the most important characteristics of population dynamics for the principal species, including periodicity and magnitude of reproduction, and maximal and minimal densities during the yearly cycle.

The first part of this study, included in the International Biological Program from 1969 to 1972, occurred during an extreme drought which peaked in 1972. Rainfall since that time, although still below 30-year averages, has increased throughout the Sahel. Biological phenomena have thus undergone a renewal, illustrated by the more or less generalized outbreaks of insects and especially rodents in 1975–1976.

The purpose of the present report is to describe this latter phenomenon in a natural environment and to establish a qualitative and quantitative comparison with observations made during the period of drought. These observations were localized to the Sahel savanna of Fete-Ole, in northern Senegal (northern Ferlo).

Average yearly rainfall of about 300 mm supports a dry bush savanna, established on old dune reliefs whose topography governs the distribution of vegetation, which includes large grassy areas with occasional trees on the dunes and dense bushy undergrowth in interdune depressions.

The rainy season lasts only three or four months, between July and October. The rest of the year is dry, becoming chilly from November to March and hot from April to June. Rainfall from 1969 to 1976

is shown in Table 1. Biological activity is concentrated in the rainy season and the first part of the dry season. The majority of the animals reproduce during this period. Animals with an annual cycle, such as rodents, generally reach their abundance maximum between October and January. Population densities then decrease, reaching their minimum just before or at the onset of the rains of the following season. The characteristics of a given annual cycle are thus functions of both the minimum density of the preceding year and the peculiarities of the present reproduction (length and fecundity), all of which determine the growth level of the population and thus the maximum annual number of individuals in the population.

The rodent population of Fete-Ole was studied from 1969 to 1972 and the population dynamics of the most abundant species, *Taterillus pygargus*, was established (Poulet, 1972a, 1972b). Other studies concerning the effects of the drought were performed in 1972 and 1973 (Poulet, 1974). The spectacular change in the rodent population was studied

Table 1.—Annual Rainfall in Fete-Ole from 1969 to 1976 (in mm).

Year	Amount of rainfall
1969	321
1970	209
1971	202
1972	33
1973	209
1974	316
1975	311
1976	343

extensively from 1975 to 1977 by samplings performed during the dry season in order to obtain information concerning the fauna and demography of

the region. The detailed analyses of these data are forthcoming (Poulet and Poupon, 1978; Poulet, in preparation).

DISCUSSION

Rodents of Fete-Ole

Gerbillidae.—The most common rodents on the Fete-Ole Sahel are *Taterillus*. *T. pygargus* is found in all the habitats, but this species is the only one which is capable of permanently occupying the dunes, because it is particularly adapted to the sandy habitat. *T. gracilis*, which is much more rare, inhabits only the bushy depressions. The two species coexist in these depressions, but *T. pygargus* consistently is the dominant species. This situation explains why *T. gracilis* appears to have virtually disappeared during the drought, a condition that is much more unfavorable to it than to *T. pygargus*.

Desmodilliscus braueri is a small subdesert rodent, which is very difficult to study because it does not enter the traps. Its presence is known by its occurrence in pellets of owls and, although difficult to trap, it may be stalked at night and caught by hand. Its abundance apparently varies inversely with that of all the other rodents; it is rare during periods of abundant rainfall and becomes more numerous during droughts. It seems to have disappeared since the outbreak of the other rodents in 1975–1976.

A *Tatera* with 52 chromosomes appeared in 1976 at the latitude of Fete-Ole but its occurrence must be considered as exceptional. Its appearance seems to be exclusively related to a temporary extension of the area of distribution of the species toward the north following the outbreak of 1975–1976.

Muridae.—*Arvicanthis* and *Mastomys* are usually not found in the Fete-Ole Sahel; *Arvicanthis niloticus* normally inhabits the campsites of nomads and *Mastomys erythroleucus* is occasionally found in certain permanent settlements of the Sahel. *Arvicanthis* invaded the Fete-Ole savanna in the rainy season of 1975. Family groups inhabited all the depressions with bushy covering and often adopted a diurnal arboreal behavior. *Mastomys erythroleucus* also inhabited the depressions but was less abundant than *Arvicanthis*. The samples taken revealed only several individuals per depression.

Pullulation of Taterillus

Following the rains of 1974, thus two years after the great drought, the rodent density had risen to

a level comparable to that of 1969–1971. There are no precise data for this period but the several *Taterillus* captures made indicated a considerable reproduction beginning in the months of October. The possibility of a rapid growth of rodent populations was indicated by the abundance of herbaceous vegetation as well as acridian multiplication. Population samplings were undertaken in January–February, April, and July of 1975 and then in February, April, and June 1976 (Table 2).

A maximum of population density was reached in April 1975, with approximately 40 *Taterillus* per ha. The reproduction season, at least 6 months long, resulted in the appearance of two successive generations, thus considerably increasing the population density. The period of population decrease resulting from the arrest of reproduction at the end of the dry season was very brief; from July 1975 onward, reproduction recommenced at already high densities, approximately 30 individuals per ha with an average of eight young per litter.

Considering an overall mortality rate of 15 to 20% per month and two successive litters of eight and six young with a starting density of 30 per ha, we may calculate an average maximum density of 180 (135–250) at the end of September. The demographic analysis of samplings of February 1976, show that reproduction during the rainy season of 1976 was indeed very short and that no new individuals appeared beginning with early October 1975. The period of population decrease in 1975–1976 was thus very long (October 1975–August 1976) and the population density decreased from 70 per ha in February to 30 in July, representing an overall mortality rate of 25% per month.

The 1976–1977 reproduction season began rather late, toward the end of September. The annual minimum density was reached at this time, with 20 individuals per ha, a level which is still considerable. The pullulation period could be considered as virtually terminated, because the following cycle showed neither as great a difference between minimum and maximum densities nor as rapid a variation of numbers of individuals.

The pullulation thus occurred in two stages—1) a progressive but important rise in the population

Table 2.—*Estimation of densities and biomass of Taterillus pygargus on the dunes of Fete-Ole during the rodent outbreak of 1975–1976. Average weight of an individual is 36 g.*

Date	Density (individuals/ha)	Biomass (g/ha)
January–February 1975	29	1,044
April 1975	40	1,440
July 1975	28	1,008
February 1976	86	3,096
April 1976	54	1,944
June 1976	28	1,008

level, due to a very long reproductive season, followed by a period of population decrease which was too short to bring the density to a low level (1974–1975); and 2) a following reproductive season characterized by a highly elevated fertility which affected the already elevated population level. The outbreak ensued and the population was quadrupled from the first litter (1975–1976).

The abrupt population increase during the second phase led to an overpopulation whose first and foremost effect was to rapidly block reproduction. Because the vegetation did not yet have the time to be degraded, the block had to be at the behavioral level; the promiscuity of individuals was reduced, thus inhibiting all subsequent gestations.

In spite of the abundance of *Taterillus*, mortality during the entire period of population decrease remained limited to a low level of 20% per month. There were no changes in the size of each age group noted between the beginning and the end of the dry season; there was thus no state of famine.

The *Taterillus pygargus*-Sahel savanna relationships appear to be especially well in equilibrium. Just as the great drought of 1972 had no irreversible consequences for the *Taterillus* population, the rapid reproduction of 1975–1976 did not lead to any considerable degradation of the habitats. It may be

considered that *Taterillus pygargus* is very suitably adapted to the dry bush environment of the Senegalese Sahel. This does not, however, mean that the outbreak of *Taterillus* was without repercussions. Seed productivity in the savanna and the details of the granivorous diet of rodents are poorly known. It is not possible to precisely estimate vegetation changes, which, although not spectacular, could nevertheless be important. Furthermore, the competitive relationships among consumers were probably changed. Thus, the exceptional abundance of rodents could furnish an explanation for the disappearance of all reproduction among certain granivorous birds, which previously reproduced quite satisfactorily at the end of the dry season (the case of certain species of turtle-doves; G. Morel, personal communication).

Invasion by Arvicanthis niloticus

The invasion of the Sahel savanna by *A. niloticus* at the end of the 1975 dry season resulted from massive migrations induced by an overpopulation at the moment of the maximum population density at the first phase of the pullulation in cultivated areas and in the villages where *Arvicanthis* lives permanently.

The intense reproduction of the newcomers, inhabiting the bushy depressions, explains the spectacular increase in the number of *Arvicanthis* between October and December 1975. The dietary requirements of a population exceeding 100 individuals per ha of habitat and a resulting biomass greater than 11 kg, are such that a state of famine could not be long in developing. The consequences of this chain of events were a significant reduction in physical parameters of the individuals of a given age (size and especially weight), a lifespan not exceeding 9 months due to an intense mortality and a very clear degradation of the woody stratum. Mortality was amplified by predation resulting from abnormal concentrations of diurnal Palearctic birds of prey.

Table 3 shows the population densities in the Sah-

Table 3.—*Estimation of densities and biomass of rodent populations of "bushy depressions" in 1976. Taterillus sp. represents T. pygargus and T. gracilis in a 60:40 ratio. Values are given in ha of effective biotope, that is, ha of bushy depression.*

Date	<i>Taterillus</i> sp.			<i>Arvicanthis niloticus</i>		
	Density/ ha	Average wt (g)	Biomass/ ha (g)	Density/ ha	Average wt (g)	Biomass/ ha (g)
February 1976	66	38	2,508	100	112	11,200
April 1976	32	38	1,216	73	98	7,154
June 1976	15	38	570	17	84	1,428

Table 4.—*Maxima and minima of population densities, in number of Taterillus pygargus per ha of Sahel savanna, for each annual cycle from 1969 to 1977. The average value of population density is calculated from the maximum assuming a constant decrease of 20% per month until the minimum. The average weight of a T. pygargus is estimated as 36 g and its daily seed consumption at 3 g. x = very low density.*

Date	Annual maximum		Annual minimum		Average density	Biomass (g)	Seed
	Date	Density	Date	Density			
1969–1970	April 1970	9	August 1970	4.1	6	216	6,480
1970–1971	October 1970	7.8	August 1971	0.6	3.2	115	3,456
1971–1972	November 1971	0.7	?	x	0.3	11	324
1972–1973	—	—	—	—	x	—	—
1973–1974	—	—	—	—	?	—	—
1974–1975	April 1975	40	July 1976	30	29.5	1,062	31,860
1975–1976	September 1975	180	September 1976	20	83	2,992	80,773
1976–1977	December 1976	45	July 1977	10	23.4	842	25,272

el depressions during the dry season of February to June 1976 for *T. pygargus* and *T. gracilis* (in a 60:40 ratio) and for *Arvicanthis niloticus*. The invasion was massive but was reduced very rapidly. In reality it affected only the “pond” biotope (bushy undergrowth in depressions), which represents only

10% of the Fete-Ole surface. It may be concluded that the permanence of the *A. niloticus* population in the dry bush savanna is questionable, which is fortunate for the natural environment as it can tolerate the presence of these murids for only a short time without irreversible damage.

CONCLUSIONS

The frequent droughts in the Sahel do not enable permanent populations of murids to be maintained in the dry bush savanna. The particular circumstances of an exceptional demographic outbreak are required for the murids to invade this zone. These new populations are nonetheless not capable of maintaining themselves, because of the unacceptable disequilibrium they impart to the habitats they invade. The invasion of *Arvicanthis niloticus* and *Mastomys erythroleucus* in the dry bush Sahel savanna represents the limits of their ecological potentialities; they must be considered not as normal dwellers but rather as invaders with deleterious actions.

Taterillus, especially *T. pygargus*, are the characteristic animals of the Sahel savanna. They may undergo enormous variations in abundance without producing irreversible disequilibrium in the habitats. Table 4 summarizes data gathered between 1969 and 1977 concerning minimum and maximum population densities, biomass, and seed consumption.

Biomass was increased by a factor of 300 be-

tween the drought of 1972 and the maximum population outbreak of 1976. These are extreme cases, related to climatic extremes of the Sahel. True Sahel species are those capable of undergoing large variations in population numbers in the absence of irreversible repercussions, neither to the species itself nor to the sheltering environment. This is indeed the case for *Taterillus* but not for *Arvicanthis*.

Seed productivity of 1 ha of Fete-Ole Sahel has been estimated at 29 kg (Bille, 1977). Availabilities from previous years bring the reserve to 40 to 60 kg. These figures are largely in excess of the needs of *Taterillus* during a drought, but it must be supposed that availabilities of the environment in 1976 were at least double, because the quantity of seeds required to support a *Taterillus* population estimated at 80 per ha is about 80 kg. This represents an indirect confirmation of the opinion of Bille, according to which, after the dry period, there is “a compensatory phenomenon enabling the very rapid biological rise of the ecosystem, both for the trees and grasses.”

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This paper was communicated by Bernard Hubert.

HABITAT HETEROGENEITY AND CHANGES IN SMALL MAMMAL COMMUNITY STRUCTURE AND RESOURCE UTILIZATION IN THE SOUTHERN KALAHARI

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ABSTRACT

The small mammal communities occurring in four habitats in the southern Kalahari from 1970 to 1976 were examined. Changes occurred in species diversity, and marked fluctuations in the population densities of different species were evident. This

led to changes in habitat-niche dimensions, and the amount of habitat-niche overlap between species. Most species also showed changes in food-niche dimensions between winter and summer.

INTRODUCTION

Previous studies on small mammals in the southern Kalahari (Nel and Rautenbach, 1975) have shown that habitat selection occurs in some species, and that it is presumably related to factors such as soil texture and the amount of cover present. Trapping results also revealed that the structure and composition of small mammal communities were different in different habitats at any given time, and that within-habitat changes were common from year to year.

Additional data have allowed a more detailed analysis of changes in the small mammal community occurring in the dry bed of the Nossob River,

as well as an attempt to quantify some dimensions of the niche each species occupies. The assessment of niche dimensions is made difficult because of the constant changes in species present, and therefore (presumably) changes in manner and context of interactions between species. This inevitably would lead to changes in niche dimensions and even possibly the amount of competition for available resources. However, even though the available data do not permit an absolute picture of niche occupation to be constructed, some idea may be gained of resource partitioning by small mammals in a sub-desert environment.

STUDY AREA

A detailed description of the study area in the Nossob River valley, Kalahari Gemsbok National Park, has appeared elsewhere (Nel and Rautenbach, 1975). Briefly, it covers the low dune forming the west bank of the river, the actual riverbed (usually dry), a raised plateau, and the high dune forming the eastern bank. The low dune consists of white-red consolidated sand, with a cover of "driedoring" bushes, *Rhigozum trichotomum* Burch., some perennial grasses, and a few camelthorn trees, *Acacia erioloba* E. Mey. The riverbed, of fine consolidated silt, is flanked by tall *A. erioloba* trees, has some bushes, such as *Galenia africana* L., occurring, and usually a good grass cover. The plateau, of white calcareous sand, has a sparse

ground cover, which gradually increases where it merges into the high dune, which has a vegetation rather similar to that of the low dune.

As rainfall figures are only available from 1966 onward, average annual rainfall (272 mm) is perhaps misleading at this stage; Fig. 1 shows that over the study period the annual rainfall varied a great deal, from 110 mm in 1970 to >550 mm in 1976. Rainfall normally occurs as sharp, localized showers. As is common in desert or subdesert regions, daily and annual temperature fluctuations are severe; temperatures can drop to -10°C in winter (though seldom for more than a few nights per season) and reach 47°C in the shade in summer.

MATERIAL AND METHODS

A trapline of 37 stations, 20 m apart, and extending from the low dune, through the riverbed and plateau, and up the high eastern dune, was laid out in December 1970. Trapping sessions were generally six months apart, and during each session three traps (a Museum Special snap trap, a Victor or McGill rat snap trap, and an aluminum Sherman live trap) were put down in a 1 m radius of the trap station, and kept baited and set for 3 days and 4 nights. Taking each 12 h period as a "trapnight," this gave

a total of 21 trapnights (7 "nights" $\times 3$ traps) per station, or 777 trapnights per trap session for the whole trapline. All animals caught were removed and live captures released 3 km beyond the study area. As the width of the arbitrarily separated habitats (low dune, riverbed, plateau, high dune) differed along the transect, 10 trap stations were within the boundaries of the low dune habitat, giving 210 trapnights/session; nine in the riverbed, giving 189 trapnights/session; 11 in the plateau, giving 231 trapnights/

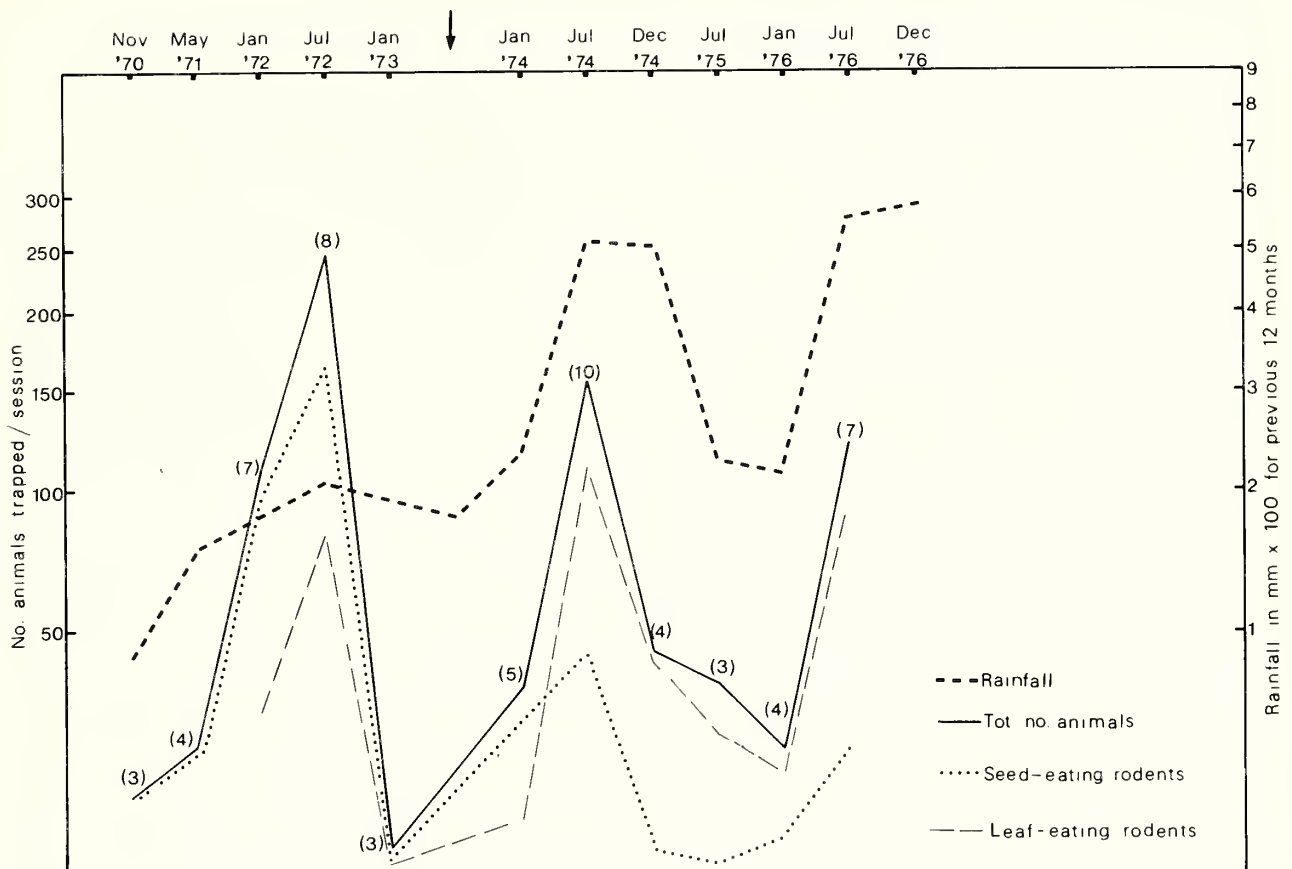


Fig. 1.—Total number, and number of seed-eating and leaf-eating rodents trapped at different periods in the Kalahari Gemsbok National Park. Number of species in parenthesis.

session; seven in the high dune, giving 147 trapnights/session. For comparative purposes, captures were recalculated as per 100 trapnights, either for particular trap stations (see calculation of habitat-niche breadth below) or for a particular habitat.

Without discussing in detail the best concept of a niche it should be noted that here it is regarded in the Hutchinsonian sense, that is being a n -dimensional hypervolume with quantification possible by measuring resource utilization along several axes. In the discussion below the niche referred to is the realized niche.

Data on distribution of the various species in the four habitats accrued from an analysis of captures at the trap stations, regarded here as each representing a different microhabitat.

Data on food preferences were obtained by analyzing stomach contents. Volumetric content and wet weights were noted, and several samples from each stomach were drawn off, shaken with water, and placed in a petri dish for subsequent determination of percentage occurrence, using a Wild M5 stereomicroscope with graticule eyepiece. In the absence of a reference collection of plant cuticles, vegetable matter was classified only as "white" (seeds, roots, and stems) or "green" (leaves). Insect material was not identified to taxonomic groups.

Activity measurements were obtained in the laboratory for only three species, during late March–April. A four-chamber,

activity-measuring cage was used (for details see Davis, 1972). Individual activity bouts were recorded on a moving strip chart in an Angus-Esterline event recorder, and subsequently analyzed as to the number of bouts per hour.

The above data were used to calculate diversity indices (and evenness of spread) for each habitat, and for the whole transect, using the Shannon-Wiener formula

$$H' = -\sum p_i \log_2 p_i \text{ in the form (after Lloyd and Ghelardi, 1963)}$$

$$H' = C \left[\log_{10} N - \left(\frac{1}{N} \sum_{i=1}^s n_i \log_{10} n_i \right) \right]$$

where $C = 3.3219$ (a constant) to convert \log_2 to \log_{10} . This measure for diversity was selected in preference to others (for example, the Broullin formula) as the data collected represent only samples of the total community (Peet, 1974).

Evenness of spread $E = H'/H'_{\max}$, where H'_{\max} is \log_2 (no. of species). Niche breadth, based on microhabitats occupied, or food taken, or times of activity, was calculated from Simpson's index of diversity

$$B = \frac{1}{\sum_{i=1}^n p_i^2}$$

where p_i represents the proportion of the i th microhabitat (or food resource, or time period) actually used; B varies from unity to n depending on the p_i values, and is standardized by dividing by n . For calculating habitat-niche breadth values, and following Krebs and Wingate (1976), data were converted to captures/100 trapnights/trap station, thus B = niche breadth, p_i = proportion of species' total density in microhabitat (=trap station) i ; p is defined from average density estimates:

$$p_i = \frac{d_i}{\sum d_i}$$

where d_i = number of individuals per 100 trapnights in microhabitat i . Standardized niche breadth for each species in any of the four habitats was then obtained by dividing by n , or the number of trap stations.

Habitat-niche breadth and overlap (see below) was calculated for each of the four habitats separately, and then for the whole transect.

Niche overlap between any two species, for a given niche dimension, was calculated following Pianka (1973):

$$O_{ij} = O_{ji} = \frac{\sum (X_{ik} X_{jk})}{\sqrt{\sum X_{ik}^2 \sum X_{jk}^2}}$$

where $O_{ij} = O_{ji}$ = niche overlap between species i and species j (range 0–1)

X_{ik} = proportion of species i numbers in resource k (microhabitat, food type, time period)

X_{jk} = proportion of species j numbers in resource k .

RESULTS

Table 1 lists the species present in the study area. Owing to the sampling technique some species were not collected in the regular trapline. For example,

most of the *Acacia erioloba* trees close to the trapline harbored tree rats *Thallomys paedulus*, but they were virtually restricted to these "habitat is-

Table 1.—Species of small mammals recorded in the study area 1970–1976. Approximate weight in grams, basic activity period, and relative density (no. captures/100 trapnights over 11 trapping periods in all four habitats) are given, as well as the habitats in which captured or seen. Abbreviation for habitats: LD = low dune; RB = riverbed; PL = plateau; HD = high dune.

Taxa	Weight	Activity	Relative density	Habitats
Order Insectivora				
Family Macroscelididae				
<i>Elephantulus intufi</i>	51.4	diurnal	0.13	LD, RB, HD
Family Soricidae				
<i>Crocidura hirta</i>	16.0	nocturnal	0.01	LD
Order Rodentia				
Family Sciuridae				
<i>Xerus inauris</i>		diurnal		RB
Family Pedetidae				
<i>Pedetes capensis</i>		nocturnal		LD, RB
Family Cricetidae and Muridae				
Subfamily Gerbillinae				
<i>Gerbillurus paeba</i>	25.9	nocturnal	3.31	All
<i>Desmodillus auricularis</i>	46.1	nocturnal	0.37	All
<i>Tatera brantsii</i>	64.9	nocturnal	0.37	LD, PL, HD
Subfamily Otomyinae				
<i>Parotomys brantsii</i>	80.0	diurnal		LD
Subfamily Dendromurinae				
<i>Dendromus melanotis</i>	6.3	nocturnal	0.08	LD, PL, HD
<i>Malacothrix typica</i>	13.0	nocturnal	0.01	PL
Subfamily Murinae				
<i>Rhabdomys pumilio</i>	32.0	diurnal	4.68	All
<i>Mus minutoides</i>	4.7	crepuscular/diurnal	0.37	All
<i>Aethomys namaquensis</i>	42.6	nocturnal	0.01	LD
<i>Zelotomys woosnami</i>	62.4	nocturnal	0.08	LD, HD
<i>Thallomys paedulus</i>	75.0	crepuscular/nocturnal		LD, RB
<i>Saccostomus campestris</i>	47.0	nocturnal	0.04	PL, HD
Family Bathyergidae				
<i>Cryptomys hottentotus</i>		?		LD
Family Hystricidae				
<i>Hystrix africae-australis</i>		nocturnal		LD

Table 2.—Relative density (no. of captures/100 trapnights) of small mammals in each of four habitats in the Nossob River, Kalahari Gemsbok National Park.

Habitat	Census period										
	Decem-							Decem-			
	ber	May	January	July	January	January	July	ber	July	January	July
	1970	1971	1972	1972	1973	1974	1974	1974	1975	1976	1976
Low dune	2.38	1.91	21.91	38.57	—	6.19	30.00	8.57	8.57	3.33	26.67
Riverbed	1.06	7.41	15.34	25.93	1.05	2.12	25.40	8.47	3.70	2.12	14.29
Plateau	0.43	—	4.76	24.24	—	0.43	9.09	—	0.43	0.87	7.36
High Dune	2.04	2.04	14.97	43.54	0.68	11.57	19.05	6.80	6.80	5.44	13.61
Overall	1.42	2.70	13.90	32.10	0.39	4.51	20.60	5.70	4.63	2.70	15.44

lands" and are therefore not reflected in the captures. Similarly, although the trapline bisected a large *Parotomys brantsi* colony during 1972, none were collected, probably due to the type of trap utilized (Nel and Rautenbach, 1976). On occasion small groups of ground squirrels crossed the census area, as did *Pedetes capensis*, but again they were not trapped. Otherwise the three trap-types used proved effective for collecting the other species present.

Fig. 1 shows that over the 6-year period December 1970 to December 1976 the total number of small mammals, as well as the number of and contribution by different species, fluctuated a great deal. Total numbers showed three peaks and three troughs, which relate fairly closely to rainfall during the previous 12 months. The low number of captures (5) in December 1976, after the study area was accidentally completely burned 6 weeks previously, obviously cannot be used for comparative purposes.

Between-habitat Variation

Although the study area was arbitrarily divided into four habitats on the grounds of differing vegetational aspects and soil types, pronounced differences were apparent in the relative density of small mammals in each habitat, and therefore its contribution to total numbers (Table 2). The plateau always had the lowest relative density, and contributed least to the community sampled by the transect. Otherwise either the low dune or high dune habitat usually had the highest relative density and contributed most. In brief, an equal or nearly equal amount of rainfall has a different effect on the productivity of the different habitats, and their ability to support different species.

The species diversity (using the Shannon-Wie-

ner index) was usually higher in the low and high dune than in the riverbed and plateau, but marked dominance by one species often resulted in very unequal distribution of total numbers among species, which resulted in a decrease of evenness in spread or *E* (Table 3). However, as the number of species (and therefore diversity) increased, in most cases, especially in the low and high dune habitats, an increase in evenness of numerical distribution between species resulted. Sometimes, however, notably from January to July 1976 in the high dune habitat, diversity remained virtually constant but evenness decreased markedly.

Changes in Community Structure and Numbers

Apart from the changes in relative density of animals in each of the four habitats, changes also oc-

Table 3.—Changes in species diversity of small mammals of four habitats in the Kalahari Gemsbok National Park. For calculations of *H'* and *E*, see methods. * = insufficient data.

Trapping period		Low dune	River-bed	Pla-teau	High dune	Over-all
January 1972	H'	0.97	0.79	0.68	0.70	1.41
	E	0.42	0.50	0.68	0.44	0.50
July 1972	H'	1.97	1.16	1.54	1.14	1.76
	E	0.76	0.58	0.55	0.49	0.59
January 1974	H'	1.88	*	*	*	*
	E	0.81	*	*	*	*
July 1974	H'	1.89	0.25	1.41	1.98	1.69
	E	0.63	0.25	0.61	0.77	0.51
December 1974	H'	0.94	*	*	1.49	1.09
	E	0.60	*	*	0.94	0.54
January 1976	H'	1.38	*	*	1.41	1.49
	E	0.87	*	*	0.89	0.75
July 1976	H'	1.38	0.73	0.52	2.09	1.38
	E	0.53	0.46	0.52	0.81	0.49

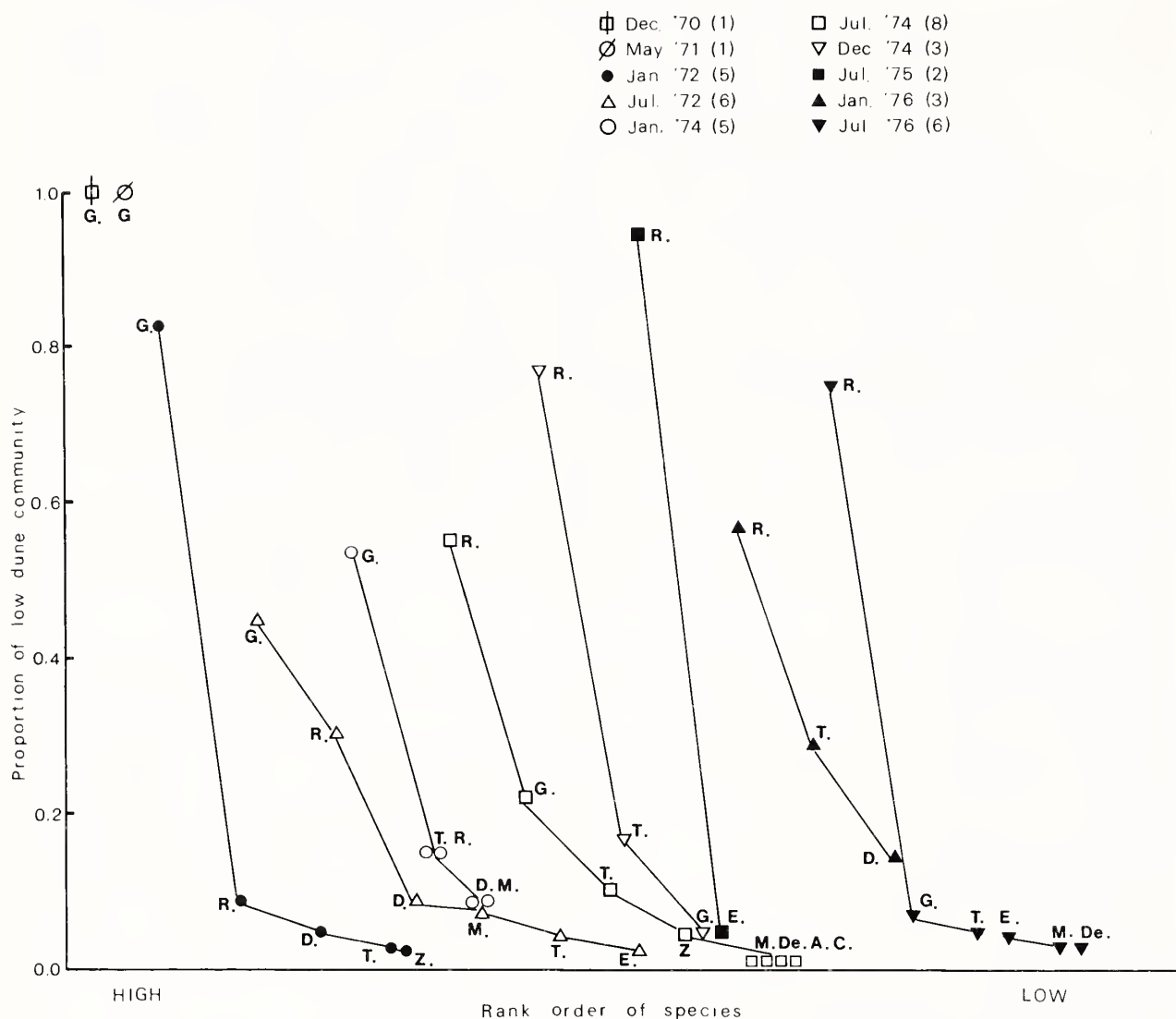


Fig. 2.—Contribution by different species to total numbers trapped at various times in the low dune habitat. Spacing of rank order of species, on horizontal axis, is arbitrary. G = *Gerbillurus paeba*; R = *Rhabdomys pumilio*; D = *Desmodillus auricularis*; T = *Tatera brantsii*; Z = *Zelotomys woosnami*; M = *Mus minutoides*; E = *Elephantulus intufi*; A = *Aethomys namaquensis*; De = *Dendromus melanotis*; C = *Crocidura hirta*.

curred in the proportion, which different species contributed to the community in a particular habitat at different periods (Figs. 2–4). On the low and high dunes, even though the number of species and the contribution by each in the community varied, the basic structure of the community remained very similar during the study period (Figs. 2 and 4). However, in the low dune community the proportions of total numbers contributed by the first and second ranking (in order of contribution) species were more fluid than in the high dune community. Over the study period, although the first or highest

ranking species usually contributed a very large proportion to total numbers in either the low or high dunes, and thus dominated the particular community, this dominant species was not always the same. Figs. 2 and 4 also show that the period during which a particular species remained dominant was different in the low dune and high dune communities; in the former, *Gerbillurus paeba* was dominant up to January 1972, then again from December 1974 to July 1975, and again in July 1976, whereas *G. paeba* remained dominant in the high dune community up to January 1974.

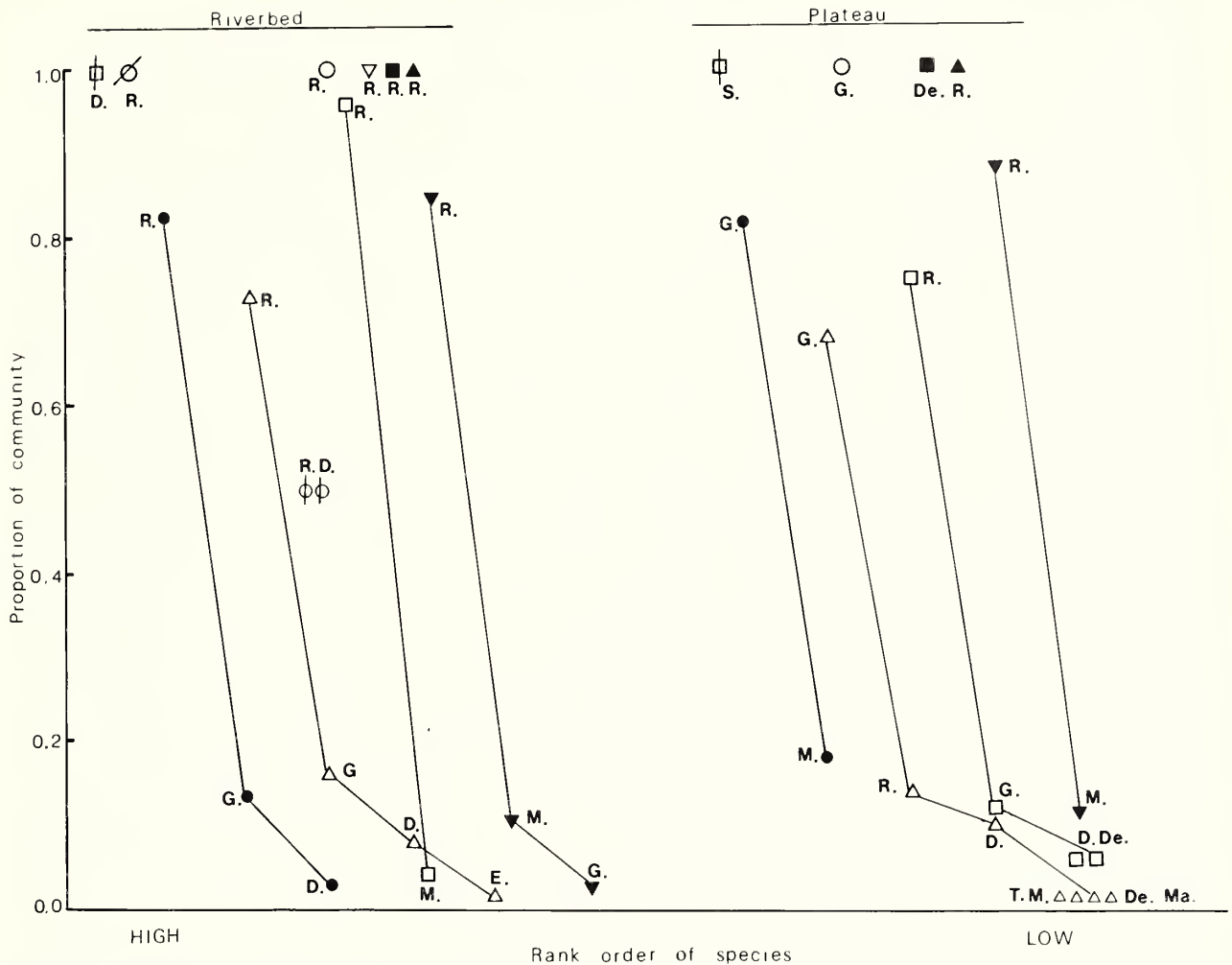


Fig. 3.—Contribution by different species, arranged in order of rank, to the riverbed and plateau communities. Ma = *Malacothrix typica*; S = *Saccostomus campestris*. Other abbreviations and symbols as in Fig. 2.

By contrast the communities in the riverbed and plateau showed a different structure. During most census periods the first-ranking species contributed nearly all the animals caught, and therefore completely dominated the community; also species diversity usually remained low (Table 3) and at times only one species was present.

It is of interest to note that the communities in the low and high dunes and riverbed (and on occasion the plateau) were primarily composed of species in the middle range of weight classes. When species numbers rose, it was the scarcer species at the bottom or top of the weight range that appeared. The selective factors mitigating in favor of a weight of 20 to 40 g in this particular environment remains, however, obscure.

Resource Utilization—Niche Dimensions

In this study, data were accumulated on only three facets of each species' niche, so that resource partitioning can only be attempted on the spatial, trophic, and temporal (or habitat, food, and time of activity) levels. As the traps were placed on the ground only indirect assessment of vertical activity or foraging levels can be attempted. Also no quantitative data are available for those species present in the study area but not trapped (see Table 1, and above).

Vertical feeding levels are shown in Fig. 5, but no quantitative data are available to allow differential utilization of various feeding levels to be assessed. Horizontal distribution is somewhat better documented, and standardized habitat-niche

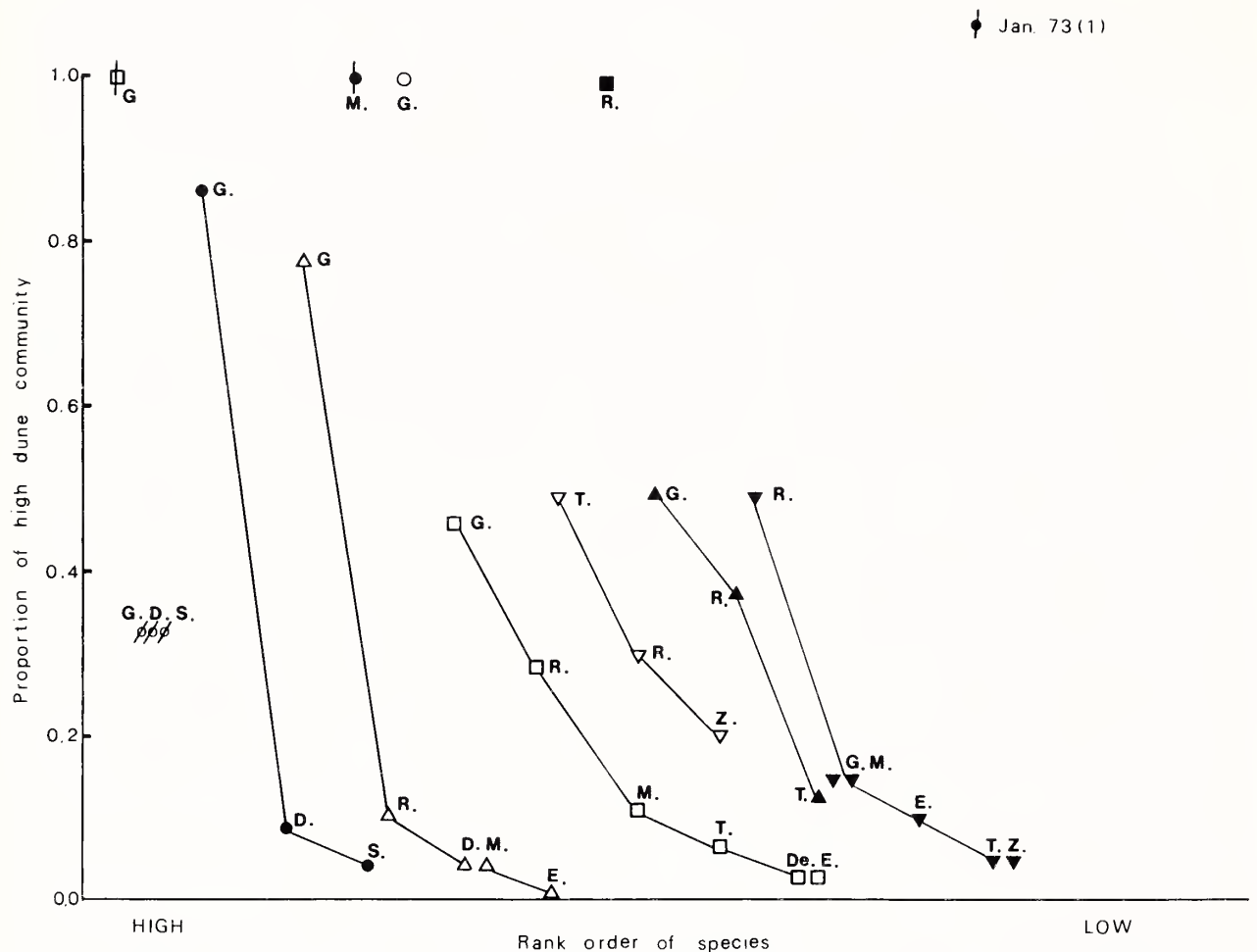


Fig. 4.—Contribution by different species, arranged in rank order, to total numbers trapped at various times in the high dune habitat. Abbreviations and symbols as in Figs. 2 and 3.

breadths, calculated as described in the methods section, are given in Table 4. As predicted by Levine (1968), niche breadth tends to increase to an asymptote as numbers rise (Fig. 6 and Table 4). As is to be expected, the more common species at any level of total number of animals or species present, for example, *G. paeba* and *R. pumilio*, tend to have wider habitat-niche breadth (Table 4), which indicates that they are less specialized and were utilizing the available habitat to a greater degree than others. The limiting factors in the habitat for any species remain conjectural, but subjectively cover seems to play a decisive role for at least some species; for example, *Desmodillus* favors very open and exposed areas, relying on acute hearing for perceiving predators (Lay, 1972), and, when rainfall and vegetative cover increases, as happened after 1972, they tend to decrease in numbers, being found

in the general area only on places artificially cleared, such as campsites. Similarly, cover, in the broad sense, affected *Rhabdomys* abundance, whereas *Thallomys*, being here confined to large camelthorn *Acacia erioloba* trees, had a very patchy distribution but probably reasonably stable numbers.

The amount of habitat-niche overlap, calculated as explained in the methods section, among the more common species at the higher levels of abundance (see also Table 2) are given in Tables 5 and 6. During periods of low numbers, species do not overlap in the habitats and/or microhabitats (distribution points) utilized. For example, in December 1970 *Gerbillurus* occurred only on the low and high dunes, *Desmodillus* in the riverbed, and *Saccostomus* on the plateau; in May 1971, *Gerbillurus* again occurred only on the low and high dunes, *Rhab-*

Table 4.—Standardized habitat niche breadth of five rodent genera trapped at 37 trap stations in four habitat types in the Nossob River, Kalahari Gemsbok National Park, from December 1970 to July 1976. LD = low dune, RB = riverbed, Pl = plateau, HD = high dune. Overall values are for transect as a whole. (—) Denotes absent from a particular habitat type during that trap session.

Taxa	Habitat	Trap session										
		Decem- ber 1970	May 1971	Janu- ary 1972	July 1972	Janu- ary 1973	Janu- ary 1974	July 1974	Decem- ber 1974	July 1975	Janu- ary 1976	July 1976
<i>Gerbillurus</i>	LD	0.36	0.16	0.80	0.75	—	0.54	0.65	0.10	—	—	0.20
	RB	—	—	0.30	0.44	—	—	—	—	—	—	0.11
	PI	—	—	0.49	0.71	—	0.09	0.18	—	—	—	—
	HD	0.26	0.14	0.69	0.88	—	0.64	0.78	—	—	0.38	0.14
	Overall	0.14	0.06	0.48	0.60	—	0.23	0.36	0.03	—	0.07	0.10
<i>Desmodillus</i>	LD	—	—	0.20	0.45	—	0.10	—	—	—	0.10	—
	RB	0.22	—	0.11	0.30	0.11	—	—	—	—	—	—
	PI	—	—	—	0.33	—	—	0.09	—	—	—	—
	HD	—	0.14	0.14	0.43	—	—	—	—	—	—	—
	Overall	0.05	0.03	0.10	0.36	0.03	0.03	0.03	—	—	0.03	—
<i>Tatera</i>	LD	—	—	0.10	0.27	—	0.20	0.23	0.18	—	0.10	0.10
	RB	—	—	—	—	—	—	—	—	—	—	—
	PI	—	—	—	0.09	—	—	—	—	—	—	—
	HD	—	—	—	—	—	—	0.29	0.40	—	0.14	0.14
	Overall	—	—	0.03	0.10	—	0.05	0.10	0.12	—	0.05	0.04
<i>Rhabdomys</i>	LD	—	—	0.27	0.57	—	0.20	0.73	0.65	0.57	0.27	0.87
	RB	—	0.42	0.50	0.77	0.11	0.30	0.84	0.43	0.26	0.30	0.53
	PI	—	—	—	0.32	—	—	0.37	—	—	0.09	0.22
	HD	—	—	—	0.47	—	—	0.68	0.43	0.60	0.43	0.60
	Overall	—	0.10	0.16	0.47	0.03	0.12	0.57	0.30	0.33	0.24	0.51
<i>Mus</i>	LD	—	—	—	0.36	—	0.10	0.10	—	—	—	0.20
	RB	—	—	—	—	—	—	0.22	—	—	—	0.33
	PI	—	—	0.18	0.09	—	—	0.09	—	—	—	0.18
	HD	—	—	—	0.43	0.14	—	0.26	—	—	—	0.26
	Overall	—	—	0.05	0.19	0.03	0.03	0.11	—	—	—	0.23

domys only in the riverbed, and *Desmodillus* and *Saccostomus* on the high dune, but not at the same distribution (= trapping) points.

During January 1974, *Gerbillurus*, *Tatera*, *Rhabdomys*, *Desmodillus*, and *Mus* occurred on the low dune; in the riverbed only *Rhabdomys* occurred and on the plateau and high dune only *Gerbillurus*. Overlap values for the low dune are as follows: *Gerbillurus/Tatera* = 0.24; *Gerbillurus/Rhabdomys* = 0.24; *Gerbillurus/Mus* = 0.33; *Gerbillurus/Desmodillus* = 0.33; *Rhabdomys/Tatera* = 0.50. Otherwise, the species present did not overlap in distribution points.

During December 1974, the only overlap was between *Gerbillurus* and *Rhabdomys* on the low dune (0.18), *Tatera* and *Rhabdomys* on the low dune and high dune (0.16 and 0.58, respectively), as well as *Tatera* and *Zelotomys* (0.67) and *Rhabdomys* and *Zelotomys* (0.58) on the high dune.

Few small mammals (apart from *Rhabdomys* only one each of *Dendromus* and *Elephantulus*) were captured in July 1975, and no overlap occurred.

In January 1976, there was overlap between *Tatera* and *Rhabdomys* only on the low and high dunes (0.41 and 0.58, respectively), *Tatera* and *Desmodillus* (1.0) and *Rhabdomys* and *Desmodillus* (0.41) on the low dune, and between *Gerbillurus* and *Rhabdomys* (0.24) and *Tatera* and *Rhabdomys* (0.58) on the high dune.

To relate amount of habitat-niche overlap to any degree of competition among species would probably be fallacious. Obviously, a high amount of overlap between *Rhabdomys* (diurnal) and *Gerbillurus* (nocturnal) may not be competition for the same resource, as this is used at different times. Probably the same applies as well to all nocturnal species, which may utilize the same place, but at different times of the night. Where a high amount

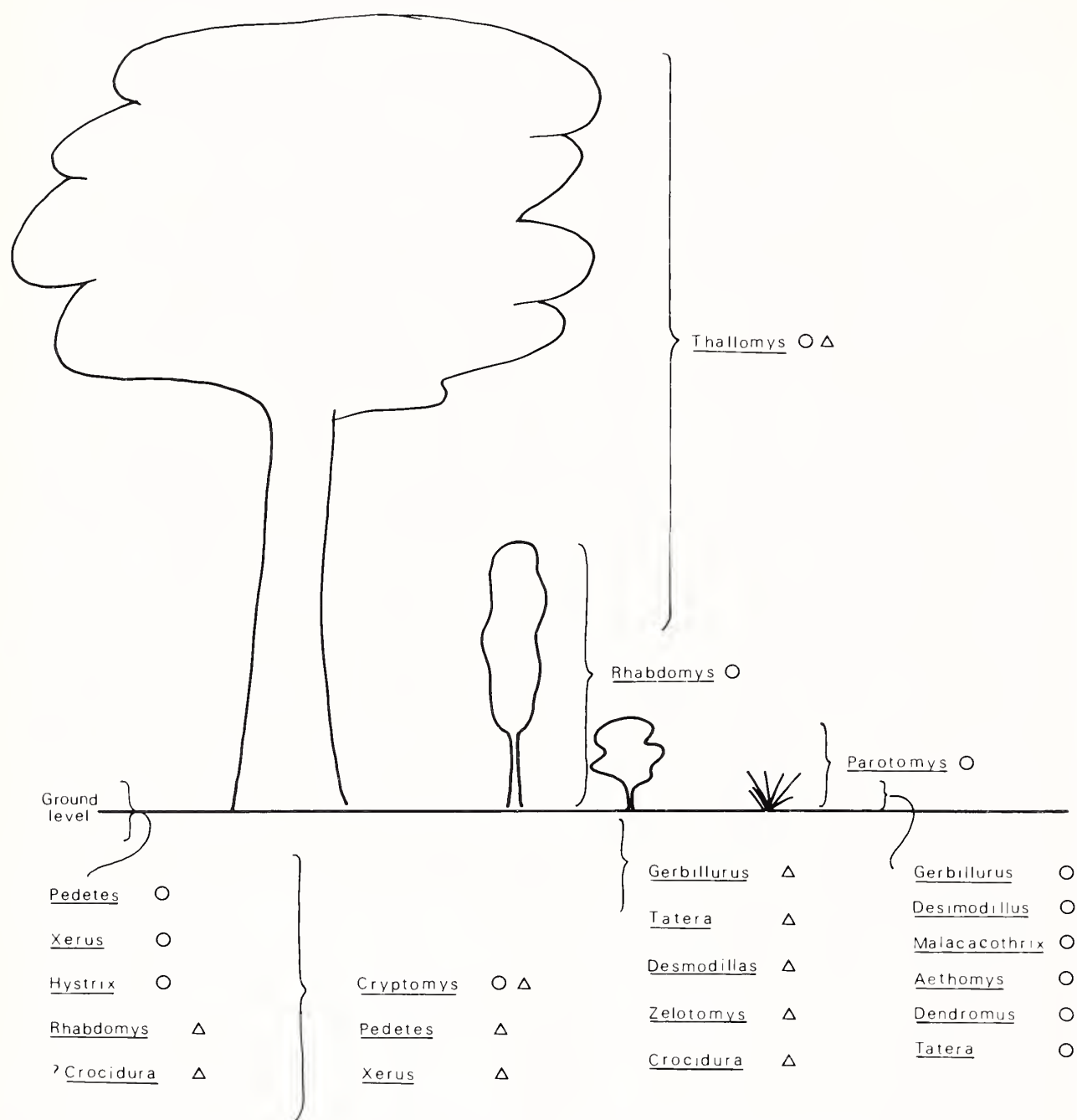


Fig. 5.—Vertical foraging levels (open circles), or level at which nesting sites occur (open triangles). Not drawn to scale.

of spatial overlap does exist (see Tables 5 and 6), different food sources in the same general area may well be utilized (Table 7). Niche overlap is perhaps better seen as an indication of the similarity of habitat (or microhabitat) favored by different species, and unless numbers reach critical heights and competitive exclusion can be demonstrated, available

space should never be at a premium. In the absence of quantitative data on plant distribution, or occurrence of areas of different foliage height diversity, however, it must remain an open question whether availability of different grades (or degrees) of cover might turn out to be a limiting factor for some species, in the presence of others.

Table 6.—Habitat niche overlap values of six rodent genera based on occurrence at 37 microhabitats, in the Nossob River, Kalahari Gemsbok National Park. Values above the boldface numbers are for July 1974 data, below are July 1976* data. For other explanations, see legend to Table 5.

Taxa	<i>Gerbillurus</i>	<i>Tatera</i>	<i>Rhabdomys</i>	<i>Mus</i>	<i>Zelotomys</i>	<i>Dendromus</i>
		.64	.55	.00	.65	.37
<i>Gerbillurus</i>	1.00	0.50	—	0.22	—	0.29
		—	0.35	—	0.45	—
		—	.64	—	—	.00
		.38	.74	.48	—	.36
	.00	—	.10	.00	.39	.22
<i>Tatera</i>	0.00	1.00	—	0.06	—	—
	—	—	—	—	0.37	0.24
	.00	—	.00	.32	—	.71
	.25	.28	—	.16	.28	.16
<i>Rhabdomys</i>	0.23	0.20	1.00	0.27	0.16	0.15
	—	—	—	.38	—	—
	.20	.20	—	.41	—	.54
	—	—	—	.43	—	.00
	.50	.00	.25	—	.00	.00
<i>Mus</i>	0.34	0.00	—	0.47	—	—
	—	—	—	.73	0.00	0.17
	.45	.00	.82	—	—	.45
	—	—	—	—	—	.00
<i>Zelotomys</i>	0.00	0.32	—	0.00	—	—
	—	—	0.05	—	1.00	0.00
	.00	1.0	.20	.00	—	—
	.50	.00	.40	.50	—	—
<i>Dendromus</i>	0.33	0.00	—	0.20	—	1.00
	—	—	—	—	—	—

* In July 1976 *Elephantulus*/*Gerbillurus* overlap on low dune by 0.32; *Elephantulus*/*Rhabdomys* by 0.34 on low and 0.72 on high dune; and *Elephantulus*/*Mus* by 0.63 on the high dune.

rainfall than did the seedeaters. The discrepancy between the numbers of seedeaters in July 1972 and July 1974, in relation to rainfall, can be explained, albeit subjectively in the absence of quantitative data, by a marked increase in cover during 1974, which adversely affected the gerbils, in particular

G. paeba and *D. auricularis*. The high numbers of small mammals during July 1972, compared to the rainfall, are more difficult to explain. However, two factors may account for this seeming anomaly—cloud cover, days of rainfall per month, temperature, and amount of precipitation per shower vary

Table 7.—Percentage of diet composed of white plant material, green plant material, or insects, of eight genera of mammals in the Kalahari Gemsbok National Park.

Taxa	Winter					Summer				
	No. seasons involved	N	% white	% green	% insects	No. seasons involved	N	% white	% green	% insects
<i>Gerbillurus</i>	2	11	76.4	23.6	0.0	3	43	39.3	43.8	16.8
<i>Desmodillus</i>	1	5	71.0	29.0	0.0	2	4	15.0	40.0	45.0
<i>Tatera</i>	3	12	67.1	27.5	5.4	3	22	34.5	59.9	5.6
<i>Mus</i>	2	10	81.0	2.0	17.0	1	1	100.0	0.0	0.0
<i>Rhabdomys</i>	2	62	31.0	58.0	11.0	2	5	18.0	72.0	10.0
<i>Zelotomys</i>	2	1		100% flesh		1	1	75.0	0.0	25.0
<i>Dendromus</i>	1	2	95.0	5.0	0.0			no data		
<i>Elephantulus</i>	1	3	8.3	0.0	91.6			no data		

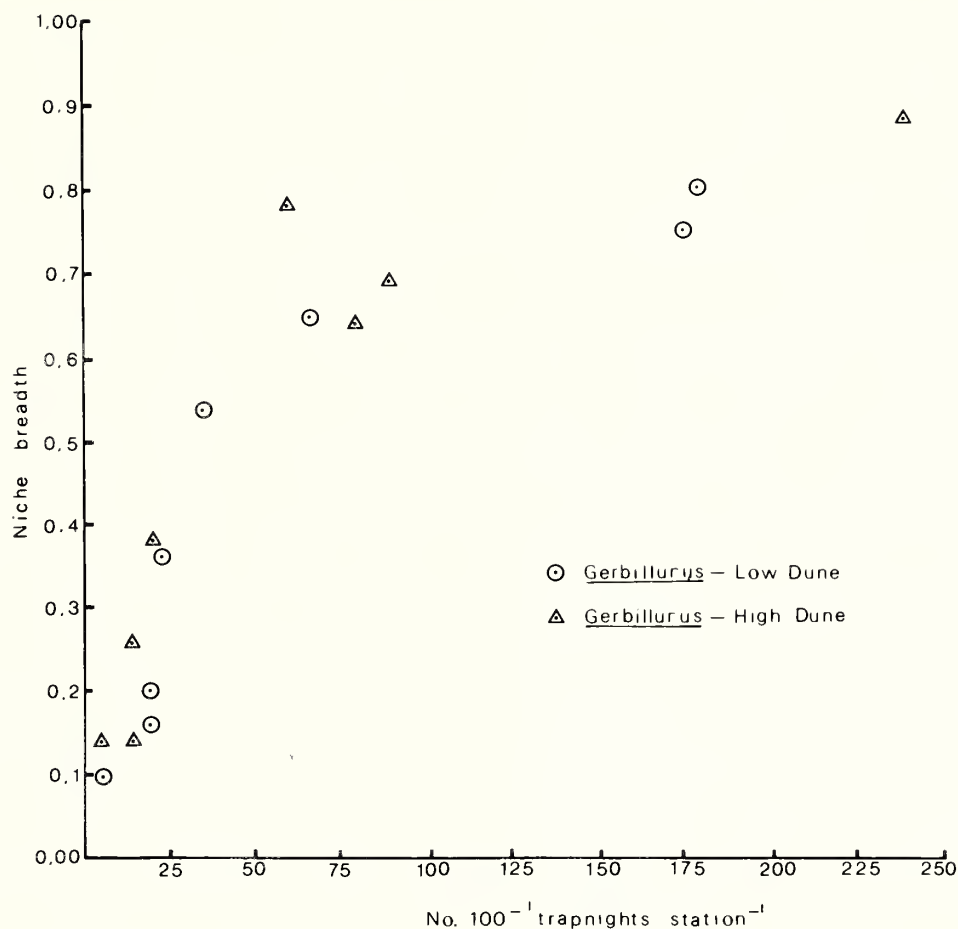


Fig. 6.—Standardized habitat niche breadth, based on 37 trapping stations of *Gerbillurus paeba* in the Nossob River, plotted against projected number of trapnights per station.

considerably and thus would affect evapotranspiration or effective rainfall, rather than actual rainfall as given here; and secondly, rainfall in the Kalahari is very patchy so that the measured rainfall during 1971–1972 may not have accurately reflected rainfall on the study area some 3 km distant.

Table 8.—Standardized food-niche breadth of eight small mammal genera in the Kalahari Gemsbok National Park, based on percentage food taken of three categories—white plant material, green plant material, and insects. Sample size given in parentheses.

Taxa	Winter	Summer
<i>Gerbillurus</i>	(11) 0.52	(43) 0.89
<i>Desmodillus</i>	(5) 0.57	(4) 0.87
<i>Tatera</i>	(12) 0.63	(22) 0.69
<i>Mus</i>	(10) 0.49	(1) 0.33
<i>Rhabdomys</i>	(62) 0.75	(5) 0.59
<i>Zelotomys</i>	(1) 0.33	(1) 0.53
<i>Dendromys</i>	(2) 0.37	no data
<i>Elephantulus</i>	(3) 0.39	no data

As the transect extended for only 720 m, rainfall was probably fairly equal along its length. Even so, various parts of the study area seem to respond differently as far as small mammal species diversity and density are concerned, which justifies subdivi-

Table 9.—Food-niche overlap values of six small mammal genera in the Kalahari Gemsbok National Park. Values above the boldface numbers are for winter, below are for summer.

Taxa	<i>Gerbillurus</i>	<i>Desmodillus</i>	<i>Tatera</i>	<i>Rhabdomys</i>	<i>Mus</i>	<i>Elephantulus</i>
<i>Gerbillurus</i>	1.00	0.99	0.99	0.70	0.94	0.09
<i>Desmodillus</i>	0.82	1.00	0.99	0.76	0.92	0.08
<i>Tatera</i>	0.96	0.74	1.00	0.77	0.93	0.16
<i>Rhabdomys</i>	0.88	0.78	0.96	1.00	0.51	0.21
<i>Mus</i>	0.64	0.24	0.50	0.24	1.00	0.29
<i>Elephantulus</i>	—	—	—	—	—	1.00

sion of the area into four distinct habitats. Differences in soil types are perhaps primarily responsible for the variation not only in plant species present and therefore food resources, but perhaps more crucially different growth forms and thus the amount and degree of cover. This would affect not only the species able to survive in a given habitat, but also the numbers it can attain in each. Whether the differences between the low and high dune habitats are real and long-term, or a result of receiving slightly different rainfall, with the resultant effects on food and cover availability, is difficult to determine; certainly the same species was not always dominant in both (Figs. 2 and 4). Certainly the low and high dunes seem more favorable to most species than the other two habitats.

As has been found for other areas as well, the community in a particular habitat comprised only a few species (in a number of cases only one) contributing the majority of animals. There are thus one abundant, a few common, and rather more scarce species present in the community, especially of the low and high dunes. In comparison the riverbed and plateau had on most occasions a depauperate small mammal fauna. However, improved conditions due to increased rainfall not only elevate numbers of species usually present, but also provide the opportunity for other species to colonize the habitats, but at very low levels of density. Due to the sampling technique employed, no real idea of distribution patterns of these scarce species emerged, but they probably exist in widely separated pieces of optimal habitat and therefore have a patchy distribution. Conditions favoring the rapid increase in numbers of wide-ranging species, and by analogy those having a wide niche breadth in any resource axis, should also permit a wider distribution and higher numbers of the usually scarce species.

Although the number of species actually recorded on the transect is surprisingly high and diverse as far as taxonomic affinities and weight class distribution is concerned, not all exist in the same habitat at the same time. The numerically dominant *G. paeba* and *R. pumilio*, even were they to compete for the same food source, do so at different times; although *G. paeba* and *T. brantsii* overlap to a large extent in their food requirements, there is little overlap in activity time and even less in their use of the horizontal plane of the habitat.

Some species separate themselves rather completely in a vertical stratification of the habitat—for example, *Thallomys* has no competitors in the top

layer of *Acacia* trees and only marginally overlaps with *Rhabdomys* closer to the ground, but at a different time of day; *Cryptomys*, being entirely fossorial, eliminates itself from competing with others effectively in this way.

The composition of the community in a particular habitat during a specific period most probably results from extrinsic factors such as rainfall, and the concomitant changes in the habitat rather than from any effects of competition between species for available resources. Viewed subjectively, increased cover favors some species (*Rhabdomys*, *Zelotomys*, *Aethomys*, *Crocidura*) while depressing numbers of others, for example *Gerbillurus* and *Desmodillus*. It is therefore clear that the composition of the small mammal community in the study area as a whole, or in particular habitats, was fluid during the study period. Presence or absence of a species probably resulted from the degree of adaptation of species to prevailing conditions.

To use the limited data available as a basis for describing the niches occupied by the various species would be rather naive. However, the data do give some idea of resource utilization by each species, though because some species were present in such low numbers results for them must remain tentative. The data do show that the species usually present, or those being more abundant, have wider niche dimensions than the scarcer or only sometimes present ones. This agrees with current ideas of niche dimensions (Pianka, 1976). The four habitats recognized (low dune, riverbed, plateau, high dune) differ in substrate composition, degree and diversity of plant cover, and to some extent slope and therefore (based on limited data available) temperature and humidity regimes. These differences affect the probability of species occurring in each habitat, and the numbers they can attain. Apart from these spatial differences, temporal changes in the habitat are brought about by variation in rainfall, but increased (or decreased) rainfall does not affect all habitats equally.

The two most common species, *G. paeba* and *R. pumilio*, are separated in the first place by their activity cycles, being nocturnal and primarily diurnal, respectively. There is also a good separation as far as the habitat is concerned, with *G. paeba* being common on the low and high dunes (patchy vegetative cover) and *R. pumilio* being more common in the riverbed, which has a dense grass cover. Increased cover, due to rainfall, restricts the occurrence of *G. paeba*, no matter which habitat is

looked at, with the reverse being true for *R. pumilio*. Diet-wise these two species are also widely separated with *G. paeba* selecting seeds in winter, but favoring green plant material and insects in summer (perhaps to offset increased evaporative loss due to higher ambient temperatures, even at night), and with *R. pumilio* being primarily a grass-eater year-round. Therefore, wherever cover is sufficiently patchy, and soil type amenable to digging, *G. paeba* occurs, whereas *R. pumilio* is totally dependent on good cover to avoid predators (see also Nel, 1975).

The two other gerbils, *D. auricularis* and *T. brantsii*, are both nocturnal, with a high amount of activity overlap between them and also with *G. paeba*. Both occur on sandy soil, but in the case of *D. auricularis* this must be firm and with very low plant cover. Although the amount of overlap in basic food resource (seeds) among the three gerbils is high, this may be more apparent than real, because of the coarse division of food and the absence of separation into seed-sizes (different-sized seeds perhaps being taken by the different-sized gerbils, as found also by Brown and Lieberman, 1973). Although low habitat-niche overlap values were recorded between *G. paeba* and *T. brantsii*, subjective assessment of the presence of *Gerbillurus* and *Tatera* burrows would indicate a much greater spatial overlap be-

tween these two genera. In the absence of quantitative data, it is difficult to say whether there is any "avoidance" effect between them when foraging, or whether trap placement (inside, at edge, or away in open from bushes) is responsible (see Brown, 1975). The only other species caught in some numbers, *Mus minutoides*, shows some spatial overlap with *Gerbillurus*, *Desmodillus*, *Tatera*, and *Rhabdomys*, but only so when total numbers of small mammals are high. In summer little food niche overlap occurs among *M. minutoides* and the others, but in winter this rises to appreciable figures. However, the very small size of *M. minutoides* probably results in very small seeds being taken, lessening competition for food with the others. The time of activity (crepuscular, diurnal) would tend to separate *Mus* from most other species apart from *R. pumilio*.

The precise factors shaping the destinies of the communities and the niche dimensions of the various species must therefore still remain conjectural at present. The data accumulated do show, however, that in an arid area such as the Kalahari, community structure and niche dimensions are plastic and constantly changing. Future work will aim at trying to explain the reasons behind this phenomenon.

ACKNOWLEDGMENTS

I am deeply indebted to Malcolm J. Coe who invited me to Oxford and acted as my host; the Council for Scientific and Industrial Research, who granted me a Senior Research bursary and travel funds; the University of Pretoria for providing travel funds, as well as those who made the gathering of data for this

paper possible. I also wish to thank Malcolm Coe and John Philipson for the many kind courtesies extended me while in Oxford, and them, as well as Wilma Crowther and Peter Woodall, for reading drafts of this manuscript and making many useful suggestions for improving it.

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NOTES ON THE FOOD AND FORAGING BEHAVIOR OF THE BAT-EARED FOX, *OTOCYON MEGALOTIS*

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ABSTRACT

Bat-eared foxes (*Otocyon megalotis*) were observed for about 180 h during 1976 and 1977 in the dry bed of the Nossob River, Kalahari Gemsbok National Park, South Africa. Observations were primarily directed toward obtaining data on the food eaten, foraging range, speed of foraging, time spent foraging, and interactions while foraging. Scats were also gathered and their contents were analyzed for species included and their percentage of occurrence. In general, invertebrates were selected as food

items with termites predominating but food selection is opportunistic. Activity of foraging and feeding depends on the season; in winter the bat-eared foxes are chiefly diurnal, whereas in summer they are nocturnal. Preliminary data indicate that feeding bouts vary depending on the season. Home ranges overlap widely, with many groups often foraging in close proximity to one another.

INTRODUCTION

The bat-eared fox, *Otocyon megalotis*, is widespread in the drier regions of southern Africa, and recently seems to have been increasing its range

(Smithers, 1971). Yet, apart from Bothma (1966, 1971) and Smithers (1971), little has been published on the food taken by this ubiquitous mammal.

METHODS

During February, July, and December 1976, and January 1977, different groups of foraging bat-eared foxes were observed in the dry bed of the Nossob River, Kalahari Gemsbok National Park, South Africa, and notes taken on food eaten, foraging range, speed of foraging, time spent foraging, and interactions while foraging. Scats were also collected at random or when following known individuals. Observations were from vehicles, with 7 × 42 binoculars, and occasionally aided at night by fog-lamps, but more usually moonlight sufficed. Detailed observa-

tions were made on a pair, with cubs, in December and January. Scats were softened in water and contents identified using a Wild stereomicroscope. Super 8-mm cine films were taken when light conditions permitted, and subsequently analyzed on a frame by frame basis.

This paper is based on limited data (approximately 180 h of observations) and should therefore be seen as an interim report from an ongoing study.

RESULTS

Food

The different food items utilized by the foxes are given in Table 1; these are from detailed analyses of samples taken from various scats. For frequency of occurrence and comparative purposes, only broad categories were used (Table 2). This table shows that in general invertebrates are selected, with the frequency of occurrence of them in scats probably reflecting availability in the areas where the scats were collected, but with termites (*Hodotermes mossambicus*) predominating. However, if the percentage contribution of various items to the total volume of the scats are taken into account, more marked differences appear. For example, although during the summer "dry" season termites constitute the bulk of scats (60 to 98%, usually >90%) from the riverbed, they form only 20 to 45%

of the volume of scats from the plateau (Nossob), probably reflecting local differences in availability of these prey items due to edaphic factors. Likewise, in the "wet" season, although termites occur in most scats, their volumetric contribution falls, but the contribution by *Grewia flava*, a small berry, rises to >50%. In January 1977, marked differences were also found between the composition of the scats from the male and female of the pair intensively followed; the female's scats were composed of 40 to 50% *Grewia*, 30 to 46% termites, and some scorpions, whereas that of the male consisted of 85% termites and about 2% *Grewia*. This discrepancy probably results from the difference in feeding range of the sexes (see below) during this period. The one and admittedly small sample of scats from the duneveld surrounding the river seems to indi-

Table 1.—Food items taken by bat-eared foxes in the southern Kalahari.

Termites	Order Isoptera; Family Hodotermitidae; <i>Hodotermes mossambicus</i>
Ants	Order Hymenoptera; Subfamily Campinotinae; <i>Camponotus fulvopilosus</i> and <i>Camponotus</i> spp. Subfamily Mirmicinae
Beetles	Order Coleoptera Family Carabidae Family Tenebrionidae Family Scarabaeidae Family Melolonthidae
Sunspiders	Order Solifugae; Family Solifugidae; <i>Solpuga</i> spp.
Grasshoppers and crickets	Order Orthoptera Family Acridiidae Family Gryllidae
Moths and cutting worms (=larval forms)	Order Lepidoptera Family Noctuidae
Millipedes	Order Myriapoda
Scorpions	Order Scorpionida

cate a somewhat different diet, again probably reflecting between-habitat differences in food availability.

In contrast to the findings of Bothma (1971) and Smithers (1971) very few vertebrate remains were found in the feces. It would appear therefore that

termites form an important part of the diet of bat-eared foxes in the southwestern Kalahari, being taken throughout the year. In winter, however, ants form the bulk of the foxes' diet, whereas *Grewia* berries, available in the "wet" season, are particularly favored. Indeed the female, intensively ob-

Table 2.—Occurrence of food items in bat-eared fox feces from the southern Kalahari. The number of samples is indicated below each date. Figures in parentheses are percentages.

Food items		Summer—Dry				Summer—"Wet"			
		Winter—Dry		Plateau		Riverbed		Plateau	
		Riverbed	Dunes	Riverbed	Cubitje	Riverbed	Riverbed	Plateau	Plateau
		Nossob	Nossob	Nossob	Quap	Nossob	Nossob	Nossob	Cubitje
		July 1976	July 1976	December	December	Early	Middle	Middle	Early
		98	7	94	54	54	30	32	13
Invertebrate	Termites	76 (77.6)	7 (100)	94 (100)	54 (100)	54 (100)	29 (96.7)	32 (100)	13 (100)
	Ants	85 (86.7)		51 (54.3)	49 (90.7)	43 (79.6)	14 (46.7)	10 (31.3)	13 (100)
	Beetles	63 (64.3)	7 (100)	84 (89.4)	54 (100)	52 (96.3)	19 (63.3)	23 (76.7)	7 (53.9)
	Beetle larvae	2 (2.0)		21 (22.3)	53 (98.2)	27 (50.0)	16 (53.3)	15 (46.9)	8 (61.5)
	Sunspiders	1 (1.0)	7 (100)	8 (8.5)	6 (11.1)	6 (11.1)	3 (10.0)	5 (15.6)	6 (46.2)
	Grasshoppers	33 (33.7)	7 (100)	5 (5.3)	3 (5.6)	3 (5.6)	4 (13.3)	2 (6.3)	
	Moths/worms	17 (17.4)		7 (7.5)	13 (24.1)			1 (3.1)	
	Scorpions					1 (1.9)	2 (6.7)		1 (7.7)
Vertebrate	Millipedes				1 (1.9)		2 (6.7)		2 (15.4)
	Hair	26 (26.5)	7 (100)	14 (14.9)	3 (5.6)	1 (1.9)	5 (16.7)	2 (6.3)	
	Bones	9 (9.2)	7 (100)	7 (7.5)					
	Feathers	4 (4.1)		5 (5.3)					
Vegetable	Grass	90 (91.8)	7 (100)	93 (98.9)	54 (100)	54 (100)	26 (86.7)	32 (100)	13 (100)
	Seeds	74 (75.5)		9 (9.6)	8 (14.8)		4 (13.3)		
	<i>Grewia flava</i>					23 (42.6)	18 (60.0)		11 (84.6)

served, would (in January) head early each evening straight for some *Grewia* bushes, browse for a while, and then continue foraging.

Foraging Time, Speed and Area

Activity (mostly spent on foraging and feeding) varies through the year and is perhaps related to thermoregulation. In winter, bat-eared fox groups in the riverbed are active by day, from approximately 0600 h up to 2000 h with a peak in foraging from 1200 h to about 1700 h. All groups flushed at night were lying down and presumably sleeping. In midsummer (December–January) on the other hand, the activity cycle was reversed, with individuals active from about 2000 h to about 0830 h, and slightly later if the day was overcast. Occasionally individuals were seen active as late as 1045 h, but this is exceptional. Especially in the late afternoons (1700 h) individuals would occasionally venture from dens, forage desultorily with evident signs of overheating for periods up to 15 min, and then return either to shade or the den itself. By mid-February foraging starts at 1600 h, and continues until about 0900 h, so it would seem that seasons impose a gradual shift in the activity cycle one way or the other.

The difference in the time spent foraging by a male and female with cubs, during December and January, was marked. The female would suckle the young before commencing foraging, and would then forage constantly for about 9.5 to 10 h before returning to the den to suckle the young; during this time away from the den she might spend about 15 to 30 min resting or grooming. After suckling the young in the morning she would forage for another 1 to 2 h, usually close to the den. The male, by contrast, forages for 3 to 4 h, and always close to the den; when not foraging, he lies at the den entrance. When the young first start foraging the male would forage alone for an hour or so, from 2000 h onwards, return to the den and accompany the cubs for 1 or 2 foraging trips, with a total time of around 3 h (data for early January). It seems probable therefore that as the cubs grow the time spent foraging by the male would gradually increase as the cubs increase their own foraging and rely less on suckling. Although data is available from only three dens it seems probable that this trait is common to bat-eared foxes in this region—the male guards the young and initiates them into foraging. Apart from suckling the young, all the female's time is taken up foraging, imposed by the rigors of nursing and

the necessity to obtain enough nourishment for herself.

No regurgitation of food for the pair-mate at the den or the cubs was ever witnessed, nor was any food caching observed.

Suckling time also seems to decrease as the cubs grow older—a pair of very small cubs suckled for 7 min at Grootkolk on 3 December 1976; at the specific den we observed constantly near Nossob camp suckling continued for 7 min on 12 December 1976, 4 min 24.5 s on 4 January 1977, and for 3 min 50 s on 6 January 1977. Whether suckling in the den by day occurs is unknown; certainly when the cubs are very small this is the rule. As they grow suckling, at least in the late afternoon and early morning, takes place at the entrance to the den with the female standing up, hind legs slightly splayed, while the cubs more or less hang from the nipples as they suckle. Suckling from at least two different nipples by an individual cub during a single feeding bout is common. Suckling, with the female lying down, was never observed; if the cubs were still very small and tried to suckle while the female was recumbent, she would get up and disappear down the den, followed by the cubs.

Limited data suggest that the foraging range is to some extent dependent on group size; a group of 10 individuals followed for 3 days in February ranged over 1.5 to 2 square km, whereas the female closely observed in December/January had a foraging range of <1.0 square km, with that of her mate considerably less. Foraging areas tend to shift slightly over time, and those of neighbouring groups overlap widely. No defense or marking of foraging areas was ever seen; by contrast, up to 15 individuals (from four groups) have been seen foraging close together in an area of less than 0.5 square km. Foraging "speed" varies greatly, obviously depending on food availability; during February 1976, for a group of 10, this varied between 0.5 to 1.2 km/h. The female already referred to above foraged about 0.5 to 2 km/h, and usually moved about 12 km per night during the course of her foraging.

Feeding Bouts

Observations indicated (see below) that when actually feeding the position of the ears changes, from being directed forward to being pulled back. The time-interval between the flipping back-flipping forward again was taken as the duration of a particular feeding bout. It was often not possible to see an animal actually chewing, especially at night or when

Table 3.—*Number and duration of feeding bouts of bat-eared foxes in the southern Kalahari.*

Season	Time	N	No. bouts/ 15 min	Mean duration (s)	Range (s)	Prey
Winter "Dry"	1500 h to 1700 h	7	81.5	7.6	1–46.0	Termites
Summer "Dry"	2000 h to 0415 h	9	50.6	7.1	1–58.1	Mainly termites
Summer "Wet"	2000 h to 0835 h	13	40.0	3.5	1–22.9	?

the mouth was obscured by vegetation, but the ears were always visible. Table 3 summarizes the limited data on number, duration, and range of duration of feeding bouts by bat-eared foxes at various periods and times of day. The only continuous recording of feeding in a particular animal was in December 1976 on a known female; for that particular night (6–7 December 1976) it appeared that after the initial intensive feeding a somewhat more slack period in feeding happens near midnight; during this time extensive self-grooming took place. Thereafter both the number and duration of feeding bouts increased, but not to the previous level. However, a great deal of variation in number and duration of feeding bouts at a particular time period, but on different days, occurs in the same animal.

Whether the decline in feeding bouts is related to increasingly less activity of prey items as the night progresses, in summer at any rate, is unknown. The known female did however show changes in the number of digging bouts/15 min through the night as follows: from 2000 to 2200 h on average 4.3 bouts/15 min were performed; from 2200 to 0500 h none at all; thereafter the incidence of digging increased sharply up to about 9 bouts/15 min after 0800 h. The male tended to have more digging bouts, perhaps necessitated by his small foraging range during the time cubs were at their den.

Foraging Behavior

When leaving the den to forage, bat-eared foxes would do so without any preliminary scouting around for possible predators. Before setting off as a group, some members may indulge in bouts of allogrooming, and this was usually the case between the male and three cubs referred to above. Large groups tend to split up into smaller groups (often pairs) during the course of their foraging, and such subgroups may be separated by up to 200 m, although they move in the same general direction. Whether the composition of these subgroups remains constant is not known. Small family groups

(two to five individuals) normally stay within five to 10 m of each other, often feeding close (<1 m) together.

The initial part of a foraging route can remain constant for a few days at a time, and this portion usually contains several deposits of feces added to every day. This may relate to wind direction; movement from the den is normally first downwind, and then for long distances (up to 1 km) crosswind. During foraging, movements tend to be erratic; straight-line movements between feeding stations of up to 50 m or more are interspersed with S-shaped runs, the latter especially evident when moving up- or downwind. When feeding stations are close together, movement is slow with frequent casting about, with often just the head and forequarters being moved as prey is taken first in front, then on the left or right side of the animal; complete turns can then occur. The fox's head is then seldom lifted, the nose remaining close to the ground surface. Movement, although in a general direction, tends to be erratic with frequent twists and turns.

When foraging, the head is held low and the ears pointed forward at about 45°. If the fox had been walking fast or running, the food source may be overshot, and, as the animal turns, the head is lowered abruptly. Otherwise the head is simply lowered even further. In all cases, when the prey is captured, the ears flip back from their front-facing position, and immediately as chewing or swallowing starts the ears point forward again. Sometimes the head is lifted when chewing or swallowing, but this is not the rule. Usually, after a few paces with the head held close to the ground and ears cocked forward, the head is lifted, back straightens, and the animal looks sideways.

On occasion, when moving at a run from one feeding station to the next, the impression is gained that the new prey source was first either heard or smelled, and then reacted to, or else it could be a known source of high prey (termites in all cases investigated) density. Certainly the movement

seems purposeful, and serves to attract partner(s) to the same spot.

Perhaps due to the high density of termites in the study area little digging, or signs of it, was seen. Although bat-eared foxes are said to take birds, I observed no interest by foxes in birds flushed or alighting near them. On the other hand, grasshoppers or even moths are actively pursued, and foxes jump into the air to catch them. The "pounce" common to other canids, for example black-backed jackal, was seen only once in a pair foraging around a grass-covered fallen tree stump. Such patches of habitat normally contain numbers of striped mice, *Rhabdomys pumilio*, and these could have been the quarry of the foraging foxes. A more attenuated

form of the pounce is seen when sunspiders are chased.

Little strife was ever noticed between pair or group members during foraging. Cubs are seldom snapped at by adults when foraging together, and this only happens when a cub would try to take a morsel away from the adult. Only on one occasion was frequent agonistic behavior seen between members of a pair; the prey items could not be identified with certainty (perhaps grasshoppers or beetles) and, while they were foraging with noses close together, one snapped at the other when the latter tried to take its prey from it. These interactions lasted about 1 to 2 s, with 12 occurring in 18 min.

DISCUSSION

The limited data available suggest that in the southwestern Kalahari bat-eared foxes subsist throughout the year almost exclusively on invertebrate prey. Although differences between the diets of individual bat-eared foxes are common, and depend to some extent on the particular habitat (for example, riverbed, plateau) occupied, seasonal trends in the diet of foxes in a particular habitat can be discerned. This results from changes in availability of prey items, and because the activity periods of the foxes shift with the changing seasons. In common with other canids, and probably also because of the rather stable home ranges, food selection is opportunistic. However, certain items are certainly preferred, especially the ripe berries of *Grewia flava*, if these occur in the home range of a particular fox. The bat-eared fox differs from other canids however in that food caching is absent—perhaps not unexpected, due to the nature of their prey.

The opportunistic nature of feeding would enhance social tolerance, as pointed out by Kleiman and Eisenberg (1973). Certainly the home ranges of bat-eared fox pairs, or groups, overlap widely and no defense of ranges was ever witnessed. In fact, many groups may forage in close proximity, utilizing the local abundance of particular prey items, such as termites. This is in contrast to the other two co-occurring canids, black-backed jackal, *Canis mesomelas*, and silver fox, *Vulpes chama*, in which mutually exclusive home ranges are found, and whose diets consist mainly of vertebrates, especially

rodents. The foraging range of these canids overlaps and the diet of the bat-eared fox in the study area perhaps reflects an adaptation to food-niche separation, in order to lessen possible competition for the same resource.

The pair-bond in bat-eared foxes, common also to other canids (Kleiman and Eisenberg, 1973), is long lasting and the male plays a major role in guarding and rearing the young. The dispersed nature of the prey items, each with low individual nutritional value, forces the female, when suckling, to forage far and for long periods. By contrast, until the cubs are old enough to accompany first the male, and then both parents, the male stays in close proximity to the den and forages for short periods only.

During the present study bat-eared fox density in the study area was high, perhaps reflecting higher insect density resulting from 3 years of abnormally high rainfall. Increased prey density would result in the female being able to find enough food to sustain suckling entire litters, and also that the male could find enough food close to the den. Conversely, in drought years both the female and male may have trouble finding enough nourishment, in the case of the female to suckle the entire litter, and in the case of the male to be able to remain close enough to the den for effective defense of the young. Increased mortality in cubs could in such cases result from either lack of food (milk), or being taken by predators, which are common in the area, or a combination of both.

ACKNOWLEDGMENTS

This paper was written while I was a Senior Visitor to the Animal Ecology Research Group, University of Oxford, made possible by generous grants from the Council of Scientific and Industrial Research. I wish to thank Malcolm Coe, my host at Oxford, for many courtesies extended me during my stay, and

to the University of Pretoria for providing funds supporting the fieldwork. Discussions with Hans Kruuk aided in the preparation of this paper, and his comments and those of Devra Kleiman on the draft manuscript are greatly appreciated.

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COEXISTENCE IN TRANSVAAL CARNIVORA

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ABSTRACT

How coexisting carnivore species avoid interspecific competition is examined by consideration of their more prominent physical and behavioral characteristics. An attempt is made to explain coexistence of the 33 Transvaal carnivore species. The behavioral characteristics, which are considered here in various combinations, are daily activity regimen, food preference, hab-

itat preference, geographical distribution, and social structure. The mean species body weight as an indicator of the size of prey on which a carnivore exists is also incorporated. Eighty-two % of the carnivores are shown to form a trend ranging from a nocturnal/solitary mode of life to an entirely diurnal/gregarious existence.

INTRODUCTION

Some two decades ago this paper might well have been titled "Niche occupation by Transvaal carnivores." The concept that each species fulfills a unique functional role in a specific place dates back to Grinnell (1924) and Elton (1927), and has served a useful function in subjectively describing the niche of an animal. However, it never really explained in detail how each animal fills its particular niche. Modern study of the niche and niche theory flows from Hutchinson's (1957) landmark paper, and allows quantification of the role each animal plays, from measurements of the amounts of various resources (axes in a hypervolume) utilized. Prior to this, Gause's (1934) experiments led to the idea that competition serves to separate species, and therefore the niches they fill. Competition through evolutionary time therefore led to separation of resource utilization in coexisting species, and the niches species occupy are therefore as much an outcome of evolution as, for example, their physical characteristics. On the other hand, although the physical characteristics of a particular species may be fairly constant over much of its distributional range, the exact niche it occupies (not in the descriptive Eltonian sense but in the analytical Hutchinsonian one) usually varies, depending on the habitat it occupies and the nature of other species in the community.

The mammal fauna of the Transvaal has been in-

tensively surveyed over the last five years (Rautenbach, in preparation). This Province possesses a particularly rich mammal fauna, consisting of 175 species of which 33 are carnivores. Adaptation and radiation has led to different parts of resources being utilized, especially food and activity periods by different members of this assemblage of carnivores. It is of interest to note how resources are shared and competition lessened, and coexistence enhanced.

Rather than work out niche occupation by the various carnivores, which to be meaningful would involve quantifying resource utilization in various axes by carnivores in specific communities, the approach here taken is to look at various attributes of co-occurring species, and then to see where and if competition may come into force. This is done by considering in combination average species mass, basic food preference, daily activity regimen, habitat selection, distribution patterns, and specific social characteristics. Trends in adaptations are also considered, especially the advantage of differential body size in coexisting carnivores preying on the same food types, as variation in body size could affect prey size taken (Rosenzweig, 1966). It was also necessary to categorize behavior, in the full realization that the behavioral scope of each species may well be wider than the particular category to which it is designated.

Table 1.—The 33 species of carnivores occurring in the Transvaal. Average body weight expressed in kg, the log. value of the mean body weight in grams, as well as the daily activity, social structure, and basic feeding categories to which each species is assigned, are indicated. See text for further explanations. I = Insectivorous, P = Predatory, O = Omnivorous, and S = Scavenging.

Species	Average weight (kg)	N	Log. weight (g)	Daily activity regimen	Social structure	Basic feeding adaptation
<i>Otocyon megalotis</i>	3.4	(7)	3.53	iii	3	I
<i>Lycaon pictus</i>	22.0	(12)	4.34	v	5	P
<i>Vulpes chama</i>	2.9	(22)	3.46	i	1	P
<i>Canis adustus</i>	10.0	(5)	4.00	ii	1	O
<i>Canis mesomelas</i>	7.8	(48)	3.89	ii	2	O
<i>Aonyx capensis</i>	12.1	(4)	4.08	iii	3	I
<i>Lutra maculicollis</i>	4.5	(1)	3.65	ii	3	I
<i>Mellivora capensis</i>	8.9	(5)	3.95	ii	2	I
<i>Poecilogle albinucha</i>	0.4	(4)	2.60	ii	3	P
<i>Ictonyx striatus</i>	1.1	(10)	3.04	i	2	I
<i>Viverra civetta</i>	12.4	(5)	4.09	i	1	O
<i>Genetta genetta</i>	1.9	(15)	3.28	i	2	P
<i>Genetta tigrina</i>	1.9	(24)	3.28	i	2	P
<i>Suricata suricatta</i>	0.7	(19)	2.85	v	5	I
<i>Paracynictus selousi</i>	1.6	(39)	3.20	i	2	I
<i>Cynictis penicillata</i>	0.8	(20)	2.90	iv	3	I
<i>Herpestes ichneumon</i>	3.1	(14)	3.49	v	3	P
<i>Herpestes sanguineus</i>	0.5	(25)	2.70	v	1	P
<i>Rhynchogale melleri</i>	2.8	(1)	3.45	ii	1	O
<i>Ichneumia albicauda</i>	3.6	(1)	3.56	i	2	P
<i>Atilax paludinosus</i>	4.3	(5)	3.63	i	1	I
<i>Mungos mungo</i>	1.3	(7)	3.11	v	5	I
<i>Helogale parvula</i>	0.2	(13)	2.30	v	5	I
<i>Proteles cristatus</i>	9.9	(14)	4.00	i	1	I
<i>Hyaena brunnea</i>	36.1	(7)	4.56	ii	2	S
<i>Crocuta crocuta</i>	69.7	(8)	4.84	ii	4	P
<i>Acinonyx jubatus</i>	35.1	(3)	4.55	iv	2	P
<i>Panthera pardus</i>	41.7	(4)	4.62	ii	1	P
<i>Panthera leo</i>	204.1	(4)	5.31	ii	4	P
<i>Felis nigripes</i>	1.5	(8)	3.18	ii	1	P
<i>Felis serval</i>	9.6	(5)	3.98	i	1	P
<i>Felis caracal</i>	10.5	(10)	4.02	ii	1	P
<i>Felis libyca</i>	4.7	(58)	3.67	ii	1	P

METHODS

Table 1 lists the 33 carnivore species occurring within the Transvaal, with average weight, expressed in kg of both sexes combined, indicated for each species. Weight data are based on Transvaal Museum records, supplemented by relevant information from Smithers (1971). Samples sizes (N) are indicated. The logarithmic values for the means of species weights as expressed in g were calculated and are also given.

Based upon personal observations and unpublished data (Rautenbach, in preparation; Nel, in preparation), as well as published information (see Smithers, 1971; Rowe-Rowe, 1977a, 1977b), an integral numerical value has been assigned to the daily activity regime of each species. These range from exclusively nocturnal with a Roman numerical value of i, to exclusively diurnal with a numerical value of v (Table 1). Categories ii and iv denote nocturnal species with some diurnal activity, and diurnal species with occasional nocturnal activities, respectively. Similarly, integral Arabic numerical values 1 through 5 have been designated for the

solitary to gregarious behavioral range, ranked from very solitary with a numerical value of 1, through to very gregarious with a numerical value of 5. The various species were each assigned to one of these five social category values on the grounds of average social grouping, allowing for other situations mentioned in the literature.

The integral values assigned to these two behavioral patterns considered (activity and social groupings) are only arbitrary points spaced along a continuum, and each represents an average categorized value considered most typical for the species. Judgment herein was subjective. We could not use more than five subdivisions with any accuracy, but in spite of this the resulting divisions are found to be both convenient and meaningful.

Hunting behavior is adapted to basic food preference. Diet and the mode of acquiring nourishment are other important aspects of the adaptive behavioral makeup of a species' accompanying avoidance of competition. Also considered in this study, then, are

the four basic feeding methods or food types of carnivores, that is scavenging, omnivorous, insectivorous (denoting a diet of any invertebrate), and predacious. In assigning each species listed in Table 1 to a feeding category, it must be stressed that carnivores are opportunistic with regard to food items taken, especially under low interspecific competitive conditions. Only what is considered to be the primary or optimum feeding trait of a species when under more intense interspecific competition is considered here.

In Fig. 1 the integral values of the activity regimen and the social structure are plotted against each other for each species. Intraspecific social interrelationships are presented on the horizontal axis, and the activity regimen on the vertical axis. In Fig. 2 the four basic feeding categories are presented by vertical columns, each of which is divided into diurnal and nocturnal subsections.

The nocturnal subsections are stippled. Each species was assigned to its appropriate column with regard to its basic feeding behavior and characteristic daily activity cycle. Position against the vertical axis was assigned by the logarithmic value of the average adult body mass, expressed in g. The principle is that clustering of species indicates possible interspecific competition, and vice versa. This is based on the correlation between the size of the predator and the size of the prey it can effectively handle, or usually catches. It has been calculated that the maximum mass of prey that can be handled with efficiency by an individual true predator is 1.5 times that of the predator itself. Group cooperation accounts for a higher ratio between the individual predator and the prey. It conversely follows that a big carnivore could not exclusively hunt very small prey because the energy gain herein would not warrant the investment in such an energy expenditure.

RESULTS AND DISCUSSION

Those species falling within the limits of behavioral values 1i, 1ii, 2i, and 2ii in Fig. 1, are all nocturnal and solitary, and represent the majority (58%) of the Transvaal Carnivora. The lines in Fig. 1 connect the upper values for both variables of this nocturnal/solitary block, with the upper values of the very gregarious and exclusively diurnal group (value 5v). All species falling between these two lines are considered to represent a trend from a solitary and a nocturnal existence to an entirely gregarious and diurnal mode of life. No less than 82% of all carnivores in the Transvaal follow this trend. *L. maculicollis*, *P. albinucha*, *O. megalotis*, and especially *A. capensis* are behaviorally intermediate between the two extremes within this trend. It is within this trend that interspecific competition is potentially the highest, as will be elaborated below. Three of the four species at the extreme diurnal/gregarious end of the trend (Fig. 1) are small insectivores and thus potentially in direct competition.

Eighteen % of the carnivore species under consideration do not conform to this trend, and have adopted a strategy, which seems to minimize possible competition. However, where four species have radiated toward a diurnal/solitary mode of life (*H. sanguineus* very successfully), only two species radiated a short distance toward a nocturnal/gregarious existence.

There are no extremely nocturnal/gregarious species (value 5i), although the lion and the spotted hyena are approaching this condition. A possible explanation for the poor radiation toward an extreme nocturnal/gregarious behavioral range could be the difficulty of maintaining group structure in the dark. Smaller gregarious species are mostly in-

sectivorous and diurnal and finding food in the dark may also present difficulties, apart from the difficulty in locating predators in time. Schaller and Lowther (1969) consider the lion, in contrast to the wild dog, as incompletely adapted to a social life because lions frequently quarrel over the proceeds of a hunt. If their interpretation is correct, the true position of the lion on the graph in Fig. 1 may be more toward the left, and consequently even closer to the general trend.

C. crocuta is basically a nocturnal animal, but may also be active during the day. According to Kruuk (1966, 1972) the species tends to scavenge by day, and to become efficient pack hunters and killers by night. The spotted hyena has a complex matriarchal social system, with the females physically bigger than the males and dominating them. *C. crocuta* thus has radiated successfully some distance away from the trend, toward a nocturnal/gregarious existence.

Otocyon, although regarded by most as a nocturnal species, has a diurnal mode of life in undisturbed areas during winter. In settled areas, however, it becomes exclusively nocturnal. In discussing the eastward range extension of the species in the Transvaal, Pienaar (1970) mentions that it is exclusively nocturnal in the Kruger National Park, and ascribes this to a form of protective behavior of colonists in a new territory. In the Transvaal as a whole the species is almost entirely nocturnal, but on the other hand it occurs for the most part in this Province only in settled areas. Studies elsewhere (Nel, 1978) show that activity is perhaps correlated to the need to thermoregulate efficiently. Most observations on the bat-eared fox in the Transvaal are

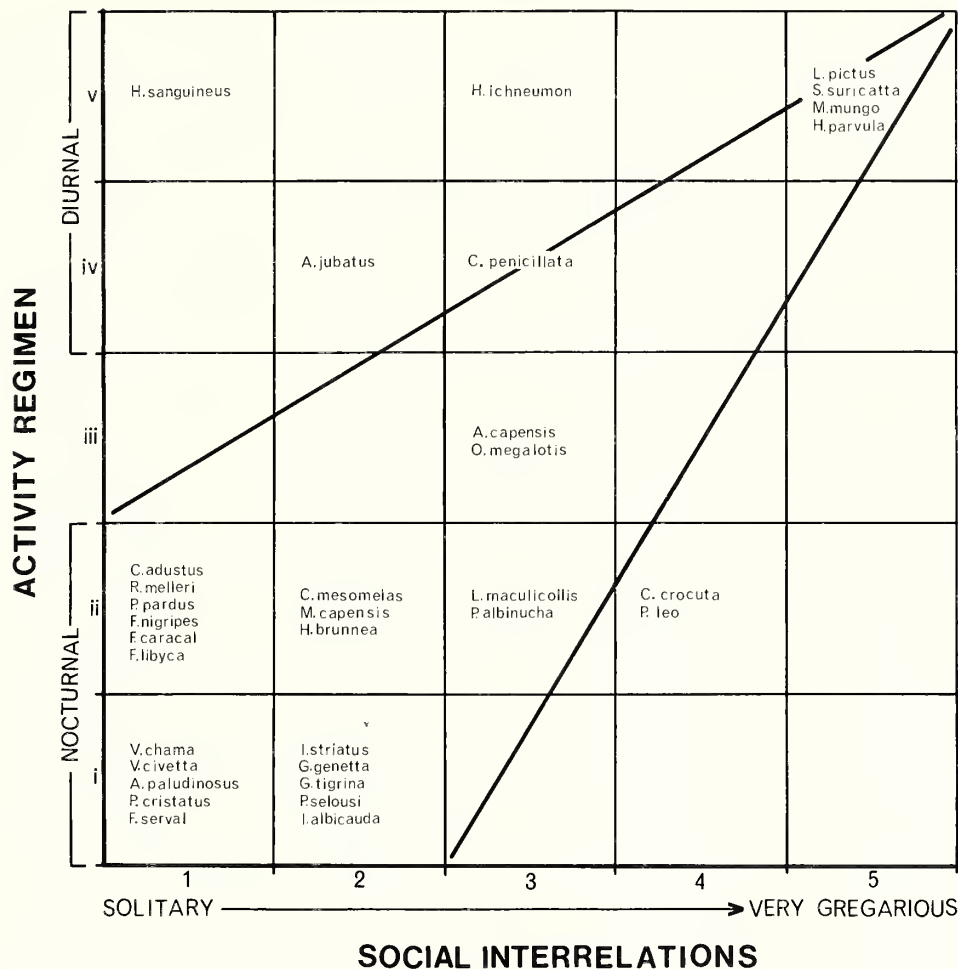


Fig. 1.—Graphical presentation of species separation by plotting the categoric values assigned to intraspecific social relations against the categoric values of daily activity cycles. See text for further explanations.

of solitary or small groups of animals, but again this would depend on the time of year of observations (Nel, 1978). This species is thus plotted in the position 3iii within the trend, although it could be argued that the Transvaal population should be plotted together with the lion just outside the trend.

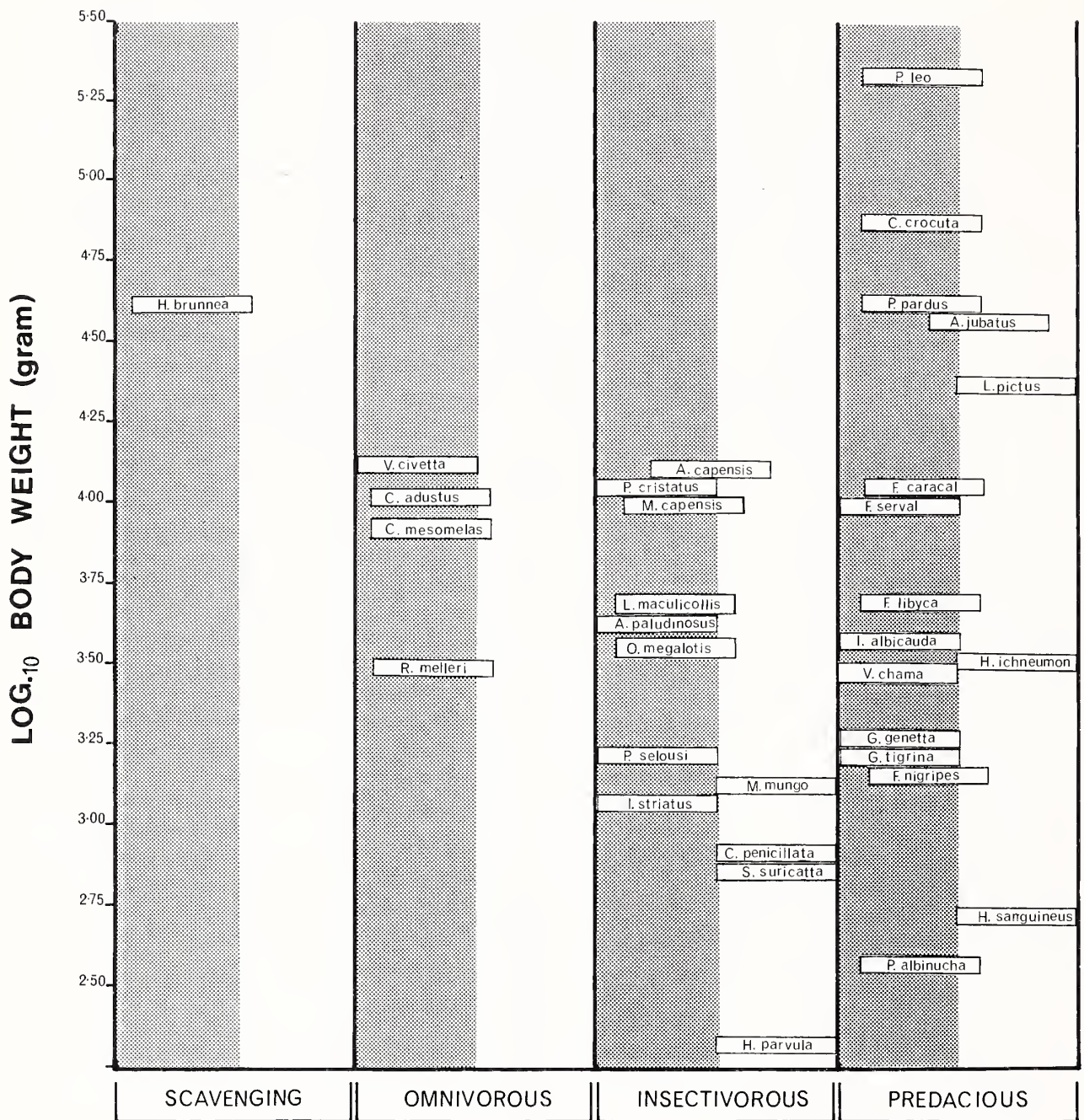
It thus would appear that a vacuum exists at the nocturnal/gregarious end of the behavioral range, but that carnivores in the Transvaal do not utilize it, for reasons at present not fully understood.

H. sanguineus is the most predacious of the Herpestinae in the Transvaal, being an efficient killer of vertebrate prey. It is furthermore solitary and diurnal, in contrast to the general tendency for the more predatory small carnivores to be solitary and nocturnal (see Ewer, 1973:277). This seeming anomaly could result from an adaptive radiation to

utilizing resources (especially habitat and food) with a low utilization pressure.

H. ichneumon and *C. penicillata* are only partly social species. When hunting for food both species are solitary and in this respect they are reminiscent of *H. sanguineus*. *H. ichneumon* is predatory, whereas *C. penicillata* is insectivorous. The distributional ranges of these two species furthermore do not overlap at all. *C. penicillata* is unique in the sense that when actively seeking food it is a solitary insectivore, in contrast to the other diurnal insectivores, which are social species.

The cheetah displays the three basic felid hunting techniques—stalking, utilization of the forepaws to fell its prey, and an oriented neck or choking throat bite according to the size of the prey. However, the cheetah atypically (for a felid) outruns its quarry



BASIC FEEDING BEHAVIOR

Fig. 2.—Graphical presentation of niche occupation. The four basic feeding categories are presented as vertical columns, each subdivided by a stippled column denoting nocturnal activity and an unstippled column denoting daylight activity. Species are assigned to their appropriate columns and are vertically spaced against the X-axis representing the log₁₀ value of the mean body weight in grams.

and possesses distinctive anatomical adaptations for this particular way of hunting, which can best be performed in daylight. There appears to be very little need for group participation. The cheetah thus

clearly acquired behavioral and physical adaptations to enable it to radiate adaptively into a less competitive area. Of the four carnivores above the trend illustrated in Fig. 1, the cheetah utilizes a dif-

ferent trophic level as a result of its larger size. Yet the survival of the cheetah is threatened. Perhaps the reason for its precarious conservation status in the Transvaal should be sought in its low ranking position in the predator hierarchy. Cheetahs are often robbed of their prey by lions, leopards, and hyenas, and are even preyed upon by these more powerful predators (Schaller and Lowther, 1969; Pienaar, 1969).

A strong bias towards the insectivorous and predacious modes of life is evident (Fig. 2). The ratio of species between the four feeding classes is 1:4:12:16. Forty-eight % of Transvaal carnivores are predacious, which is considered to be the primary feeding trait of the Order. The remaining 52% have radiated away from a true predacious existence toward utilization of other protein resources, and have behaviorally adapted themselves to procuring them. Furthermore, no less than 75% of all species are predominantly nocturnal. The mean weight of the species in the omnivorous category is 8.25 kg, that of the insectivores is 4.07 kg, and the predators 25.82 kg.

We agree with Skinner (1976) that *H. brunnea* is basically a scavenger. This is further substantiated by the special dental and cranial adaptations acquired to cope with a scavenging way of life. Such a life style is for several reasons an uncertain existence, with chance playing no minor role. This is reflected in the single species represented in this category as well as the fact that it is primarily solitary, presumably in order to avoid excessive intra-specific competition for limited resources. Considering the apparent hardships of a scavenging life style, a lower mean weight may be an appropriate manner of reducing the energy requirements of the species. However, all indications are that the brown hyena is in all aspects primarily adapted towards capitalizing on the proceeds of the hunting endeavors of the larger predators.

An omnivorous life style is seen as the most opportunistic of all, and can include as food items vertebrates (which are actively hunted), insects, carrion, and vegetable matter, especially fruit. The concept of a smaller body size as a means of reducing the energy requirements of the species with such a precarious existence can be illustrated by the fact that the mean species weight in the omnivorous category is only 8.3 kg, as opposed to the mean of 25.8 kg of the predatory category and mean of 36.1 kg of *H. brunnea* in the scavenging category.

R. melleri is much smaller than the other three

species in the omnivorous category, and from this it is concluded that overlap in feeding interests is small. *V. civetta* is ecologically separated from *C. mesomelas* and *C. adustus*. The latter two species are inhabitants of the open plains and avoid forests. Like Smithers' (1971) findings, our own observations on *V. civetta* indicate a close association with riverine and subriverine woodlands. *C. adustus* is limited in range to the eastern Transvaal lowveld and a small area north of Pretoria. *C. mesomelas* ranges throughout the Transvaal. The two species are thus partly sympatric, and as is suggested in Fig. 1 may be in conflict here. Although Shortridge (1934) and Smithers (1971) speculate that *C. mesomelas* is being gradually replaced by *C. adustus* in the overlapping zone, this could not be demonstrated in the Transvaal. According to Pienaar (1963) *C. mesomelas* is numerically the more successful species in the Kruger National Park. *C. adustus* is however slightly larger than *C. mesomelas*, and indications are that it relies less on vegetable matter as a food source.

The insectivorous feeding category has the lowest mean body weight. This is considered as a significant adaptation to the small size of the individual prey, and the quantity and effort required on the part of the carnivore to fulfill its energy requirements. There are three clusters in this category that warrant closer scrutiny (see Fig. 1).

A. capensis is the biggest member of the insectivorous group. It is an aquatic mammal subsisting almost entirely on crabs (Rowe-Rowe, 1977a, 1977b). The terrestrial *P. cristatus* is the biggest carnivore living on Insecta, namely almost exclusively termites (especially *Trinervitermes*). It is not well equipped to dig out subterranean termites. *M. capensis* is also terrestrial and overlaps in range with the aardwolf. It however hunts invertebrates bigger than termites, especially spiders. The honeybadger is particularly well adapted to procuring this subterranean prey.

L. maculicollis, *A. paludinosus*, and *O. megalotis* also form a cluster in Fig. 1. The latter species is however a terrestrial inhabitant of the open plains, whereas the former two are to varying degrees semiaquatic. The spotted-necked otter and the marsh mongoose appear to be in conflict as they both rely heavily on crustaceans in their respective diets, and furthermore overlap in geographic range and habitat requirements. *A. paludinosus* is however a more versatile animal because it is more mobile on land. It wanders greater distances away from water and

utilizes a wider spectrum of food resources. It is furthermore believed to hunt for aquatic prey only in the shallows, as opposed to *L. maculicollis*.

C. penicillata and *S. suricatta* also overlap in distributional range. Where the suricate is very gregarious and almost exclusively insectivorous, the yellow mongoose is a solitary hunter, which takes vertebrate prey as well as invertebrates.

The predatory category is the true domain of the Felidae, and no felid has radiated away from it. They are specialist killers, the only group capable of handling prey larger than themselves singlehanded. This is achieved mostly by means of a lethal well-directed single neckbite, or derivations thereof. Felidae are, in general, also expert stalkers.

Of the nonfelids in this feeding category, the mustelid *P. albinucha* is an exception, in that it behaves very similarly to the Felidae with regard to killing efficiency and the size of prey that it can handle. The remainder, that is the viverrids, canids, and *Crocuta*, all belong conditionally to the predatory category. *C. crocuta* and *L. pictus* rely on group cooperation to kill, and are relatively inefficient predators when alone. The remainder of the nonfelids rely on the other food sources already discussed, and when they kill, it is mostly prey much smaller than themselves (excluding domestic stock).

Very little is known of the serval, but from the information that is available, it would appear not to be in conflict with the caracal, as is indicated in Fig.

1. The serval appears to be restricted to areas with permanent surface water and its associated forests, and preys mostly on rodents. The caracal, on the other hand, does not prefer forests and is a true predator of prey more equal in size to itself.

The geographic ranges of *V. chama* and *I. albicauda* overlap only peripherally in the Transvaal. *F. libyca*, on the other hand, is widely distributed and overlaps with the ranges of both the former species. *F. libyca* and *V. chama* are separated in size to the extent that they presumably avoid conflict by means of differential choice in prey size. *I. albicauda* is restricted to riverine forests, whereas *F. libyca* has a wide habitat tolerance. The latter species therefore appears to be a universalist, the former a specialist extremely well adapted to its particular narrow niche. In the zone of contact between these two species, it can be postulated that *I. albicauda* has the edge in a competitive situation.

The two species of genets are partly sympatric. Our own experience agrees with that of Smithers (1971) in that these two species are ecologically separated. *G. tigrina* prefers a habitat close to water, whereas *G. genetta* exists away from it. The range of *F. nigripes* overlaps partially with that of *G. genetta*, and not at all with *G. tigrina*. However, so little is known about the general biology of the black-footed cat, that no suggestions can be offered as to how it avoids conflict with the small-spotted genet.

CONCLUSIONS

A behavioral trend is indicated in carnivores, which ranges from a direct correlation between a nocturnal/solitary mode of life, to an entirely diurnal/gregarious existence. We conclude that 82% of the Transvaal carnivores fall within this trend. Presumed adaptive radiation away from this trend is restricted to six species. Carnivores are considered incapable of adapting to an entirely nocturnal/gregarious life style.

In the majority of coexisting species interspecific

competition is avoided, primarily through different food sources, differences in size of food items (correlated to different body size of the carnivores), or differential use of habitat types. However, in the instances of the two jackal species, *L. maculicollis* and *A. paludinosus*, as well as *F. nigripes* and *G. genetta*, at least partial interspecific competition is suspected. A more intimate knowledge of the general biology of these six species may in time show more subtle mechanisms of avoiding conflict.

ACKNOWLEDGMENTS

This paper is based on a long-term intensive mammal survey in the Transvaal, a project financed jointly by the S.A. Council for Scientific and Industrial Research and the Transvaal Museum. Presentation of this paper at the Colloquium was in the case of Rautenbach made possible by funds from the Transvaal

Museum and the Department of National Education. Travel expenses for Nel were provided by the University of Pretoria and the Mammal Research Institute of this University. We express our deep gratitude to these institutions for their assistance. The manuscript was typed by Mrs. E. du Plooy.

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SYSTEMATICS OF THE HYRACOIDEA: TOWARD A CLARIFICATION

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ABSTRACT

Opinion is divided on whether the Order of the Hyracoidea contains three genera, *Procavia*, *Heterohyrax* and *Dendrohyrax*, or whether *Heterohyrax* should be regarded as a subgenus of

Dendrohyrax. The anatomical and behavioral features here presented show that there is a roughly equal, definite distinction between all three, justifying a differentiation into three genera.

INTRODUCTION

The systematic relationships of the Hyracoidea are still open to many questions. The classification at the species level is not at all clear, and there are still divergent opinions about the number of genera in this Order.

Hahn (1935, 1959), in his revision of the Hyracoidea, distinguished three genera—the tree hyrax, *Dendrohyrax*, the bush hyrax, *Heterohyrax*, and the rock hyrax, *Procavia*. In more recent reviews, Bothma (1971) and Kingdon (1971) agree with Hahn, whereas Hayman (letter dated 29 October 1964 to C. R. S. Pitman, on file in British Museum [Natural History], London) and Roche (1972) maintain that there are only two genera, *Procavia* and *Dendrohyrax*, *Heterohyrax* being a subgenus of

the latter. Roche even thinks it possible that *Dendrohyrax* and *Heterohyrax* may be merely different species; the only basis for his assumption is the small extent of cranial and especially dental distinction between these two. The molars are of brachydont structure in both, whereas *Procavia* has hypsodont dentition.

A new perspective may settle the controversy, and this paper therefore describes some anatomical features and behavioral aspects of *Procavia johnstoni matschiei* Neumann 1900, *Heterohyrax brucei dieseneri* Brauer 1917, and *Dendrohyrax arboreus stuhlmanni* (Matschie) 1892, as representatives for each genus.

METHODS

While studying the ecology and social behavior of the rock hyrax *P. johnstoni* and the bush hyrax *H. brucei* (Hoeck 1975, 1977 a, and in preparation) in the Serengeti National Park, Tanzania, in 1971–1973 and 1975–1976, over 350 animals were trapped, examined, and basic body measurements were taken before release.

Eight *D. arboreus*, living on fig trees (*Ficus natalensis*), in the

Ngorongoro Crater floor were also trapped, measured, and observed for 10 nights.

Total body length and anus-preputial opening distance were measured with the animal lying stretched on its back. The anus-preputial opening measurement of one adult *Dendrohyrax validus* male from the West Kilimanjaro Forest was kindly supplied by Mr. P. Fox.

RESULTS

Anatomical Differences

Anus-preputial opening.—This measurement allows a clear distinction between males of the three species (Table 1). *H. brucei* males have twice the anus-preputial opening distance of *P. johnstoni* males, and over three times that of *D. arboreus* and *D. validus*.

Table 1 includes, for comparative purposes, the body weight and length of adult males (over 16 months). *H. brucei* and *D. arboreus* have identical

measurements, whereas *P. johnstoni* is heavier and larger.

Penis structure.—There is a striking difference of penis structure in *D. arboreus*, *H. brucei*, and *P. johnstoni* (Fig. 1). *D. arboreus* males have a short, simply-built penis that is slightly curved. No evident difference was observed in the external penis anatomy of *D. arboreus* and *D. validus*. The penis of *H. brucei* is complex; on the penis end, and arising within a cup-like glans penis, is a short, thin

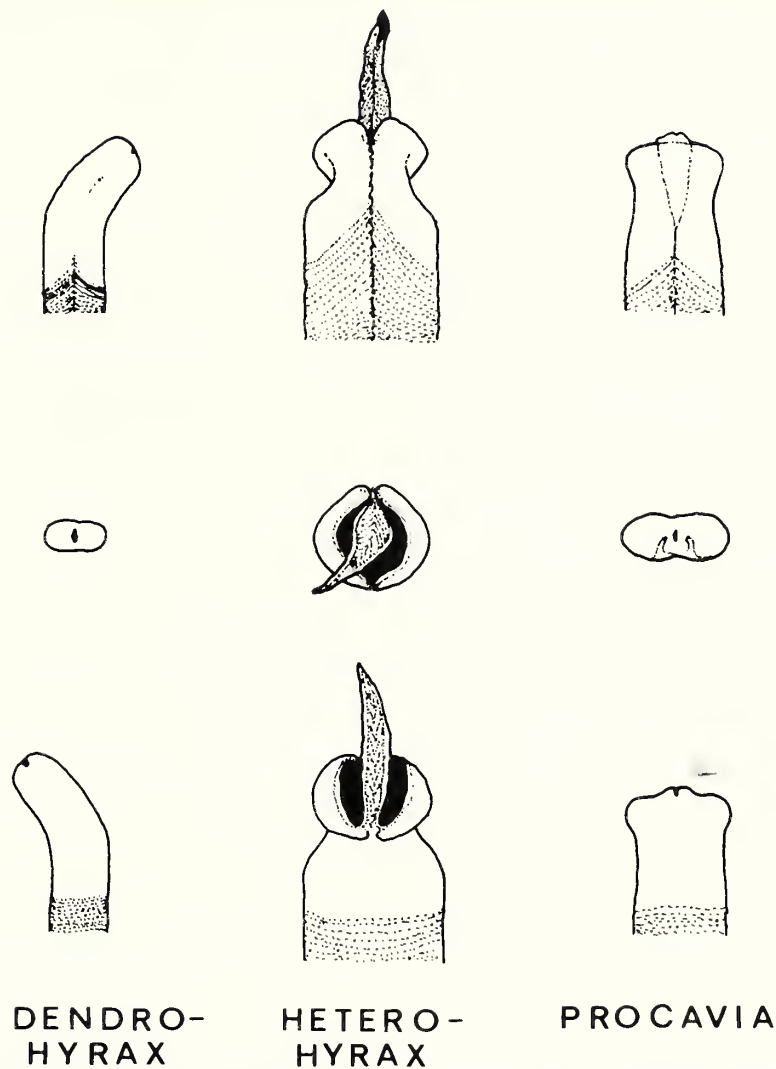


Fig. 1.—Diagram of external penis anatomy in adult males of *Dendrohyrax arboreus*, *D. validus*, *Heterohyrax brucei*, and *Procavia johnstoni*, showing approximate size relationship. Top, penis as viewed ventrally; middle, viewed from above the supine animal; bottom, dorsal view.

appendage, which has the penis opening. Fully erected, the little appendage also stiffens, the penis measures over 6 cm (Fig. 2). *P. johnstoni* have a short, simply-built penis with a slightly elliptical cross-section, the diameter increasing slightly toward the tip. More detailed features of the anatomy and histology of the penis of *Heterohyrax* and *Procavia* are given by Glover and Sale (1968).

Foot color.—The skin of the foot pads of *P. johnstoni* and *H. brucei* is black, whereas in *D. arboreus* it is pink. *D. arboreus ruwenzorii*, however, living among rocks in the Ruwenzori Mountains, Uganda, have black skin on these pads (T. Struhsacker, personal communication).

Behavioral Differences

Activity patterns and feeding behavior.—The long-term observations in the Serengeti showed that both *P. johnstoni* and *H. brucei* are diurnal. Although feeding times are identical, feeding behavior differs. *P. johnstoni* is mainly a grazer; *H. brucei* feeds almost exclusively on browse material. For further details see Hoeck (1975, 1976a, 1977b). The brief observations in the Ngorongoro Crater clearly established *D. arboreus* as nocturnal, browsing almost exclusively on *Ficus natalensis* and *Acacia albida* trees.

Mating behavior.—The following differences were observed in the mating behavior of *P. john-*



Fig. 2.—*Heterohyrax brucei* male and female just before copulation. Notice the length of the male's nearly-erected penis.

stoni and *H. brucei*, based on 14 and 21 observed copulations, respectively.

In *P. johnstoni*, usually after an initial mating call, the male executes weaving head movements, the penis is erected, and the dorsal hairs raised. The female presses her rump against the male's flank or breast. After mounting, the male grasps the sides of the female vigorously with his forelegs, makes several thrusting motions, the last being a short jerk, and then jumps down. Copulation lasts only a few seconds (Hoeck, 1976b).

In *H. brucei*, the male approaches the female, giving a short shrill call almost inaudible to humans, and both perform a short "dance" during which the male smells the vagina. He then mounts, holding the female's sides with his forelegs. With fully

erected penis the male makes several thrusting motions, while swinging the head from side to side and sometimes opening his mouth, probably calling. The penis is not introduced, but pressed against the vagina. The position being maintained, the penis slackens; after 20 to 30 seconds several renewed thrusts are made with fully erected penis, but still without introduction. After some 3 to 5 min the penis is completely introduced with a sudden violent jerk, whereupon the female jumps, bites, and chases the male (Hoeck, 1977c).

Mating was not observed in *D. arboreus*.

The territorial call.—Adult males of *H. brucei*, *D. arboreus*, and *P. johnstoni* have very distinctive calls, as shown in the sonogram (Fig. 3).

The call of *H. brucei* is shrill and long, lasting about 1.5 seconds. It is given repeatedly for up to 5 min.

The calls of *D. arboreus* start with several cracking sounds, which are followed by a loud scream, repeated several times. The sonogram shows the transition between the cracking sounds and the scream. Several short cracking sounds follow immediately after each of the first few screams, whereas in the later part of the sequence the scream occurs alone.

The call of *P. johnstoni* is a repetitious bark, becoming longer and louder toward the end of the sequence, the last barks ending with guttural noises. One of these last barks with the following guttural can be seen in the sonogram.

Calls are loud in all three species (audible for several hundred meters, depending on wind conditions), and a calling sequence may last up to 5 min. In *H. brucei* and *D. arboreus* only the adult males were observed to produce these calls, whereas in *P. johnstoni* on rare occasions adult females made similar calls. The territorial calls became more frequent in *P. johnstoni* and *H. brucei* toward the mat-

Table 1.—Anus-preputial opening distance, body weight, and total body length for adult males. Lengths were measured with the animals lying stretched on their backs.

Species	Distance anus-preputial opening (cm)			Body weight (kg)			Body length (cm)		
	N	Mean	SD	N	Mean	SD	N	Mean	SD
<i>Procavia johnstoni</i>	41	3.5	0.91	66	2.95	0.72	43	48.68	4.47
<i>Heterohyrax brucei</i>	31	8.0	0.81	57	1.75	0.17	28	43.39	1.78
<i>Dendrohyrax arboreus</i>	2	1.7		2	1.62		2	43.85	
<i>Dendrohyrax validus</i>	1	2.5							

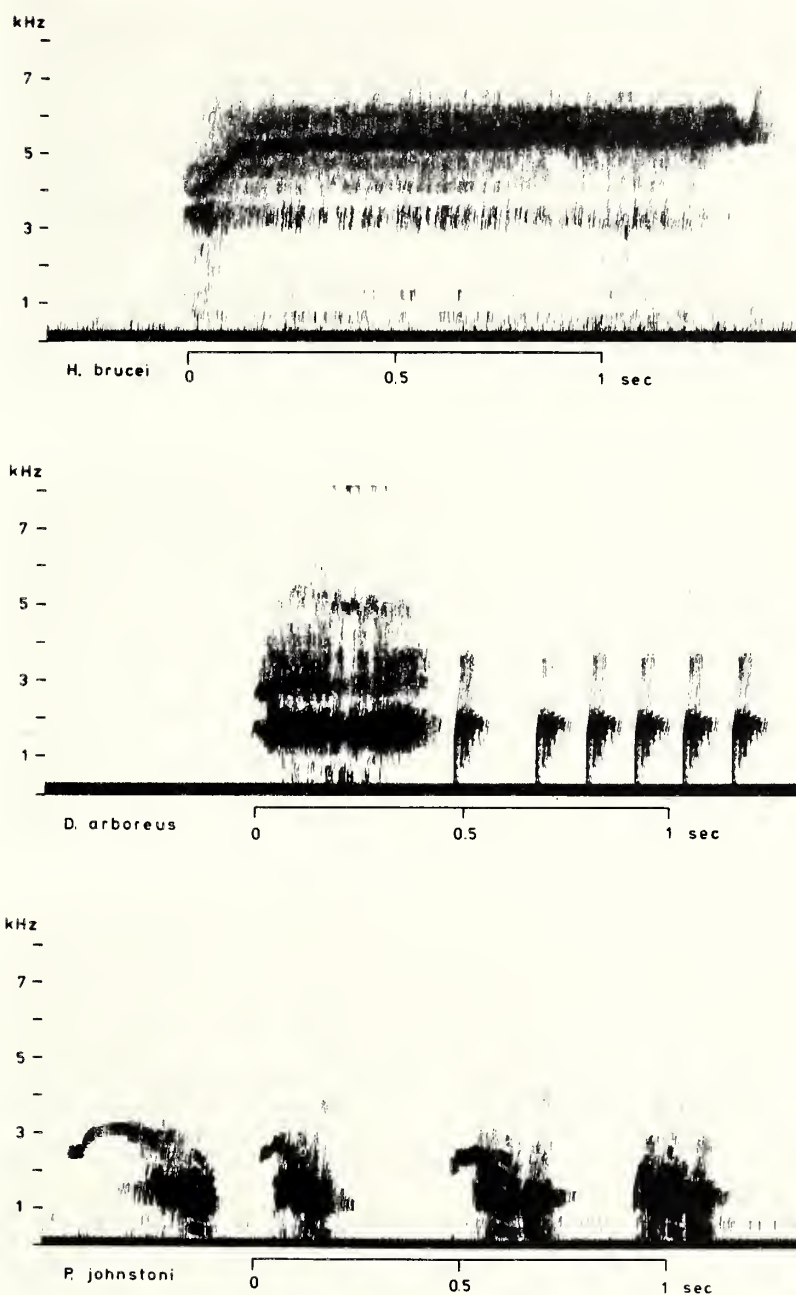


Fig. 3.—Sonograms of male territorial calls for *Heterohyrax brucei*, *Dendrohyrax arboreus*, and *Procavia johnstoni*. A calling sequence may last up to 5 min. Representative sounds from sequences are given for all three species.

ing season, and were usually made by territorial males (Hoeck, in preparation). The call of one territorial male may stimulate all others in the vicinity

to call. Each animal's calls are so distinctive that they allow individual recognition by the human observer.

DISCUSSION

The anatomical and behavioral differences presented, namely penis anatomy, anus-preputial

opening distance, and the territorial call, show *H. brucei* to be distinct from both *D. arboreus* and *P.*

johnstoni. As a browser, *H. brucei* resembles *D. arboreus*, whereas its activity pattern is identical with that of *P. johnstoni*.

Lönneberg (1916) and Hahn (1959) suggested that the variation in hyrax molar structure could be a dietetic adaptation; as grass is a relatively coarse material, grazers should be expected to have hypsodont dentition (high crowns with relatively short roots), whereas browsers, consuming softer food, should have brachydont dentition (short crowns with relatively long roots). Observation of the feeding behavior shows exactly this state of affairs. *P. johnstoni*, mainly a grazer, has hypsodont molars, whereas the browsers *H. brucei* and *D. arboreus* have brachydont dentition. If our studies are confined to a comparison of molar structure and feeding behavior, a very close relationship between *Heterohyrax* and *Dendrohyrax* seems to be established. But for a revision of the systematics of an animal group, as many taxonomic criteria as possible should be examined not only anatomical, but also genetical, ecological and behavioral parameters, to ensure accurate comparison and exact taxonomic grouping.

In a group of species the distribution of behavioral similarities and differences tend to be related with phylogenetic relationships within the group (Brown, 1975). Behavior is a preeminently suitable field for adaptation; it is regularly a pacemaker in evolution, that is, it precedes adaptive anatomical

change (Mayr, 1958; Wickler, 1972). In selecting a behavior pattern for comparative analysis, it should ideally be highly stereotyped within a species, but variable across species. Such a species characteristic behavior pattern is, for example, the copulatory behavior as shown in the comparative study of muroid rodents by Dewsbury (1975).

The territorial call is so distinct in character that it can confidently be used as a simple method of locating and recognizing different species. By this means a population of *Dendrohyrax validus* was discovered and first reported for the Kenya coast (Seibt et al., 1977).

The distance between the anus and the preputial opening, first noted by Coetzee (1966), and the structure of the penis, are important and very useful features for a rapid taxonomic identification. The females reproductive tract has not so far been analyzed, but this may also show a characteristic structure.

These observations suggest that *Heterohyrax* is as far apart from *Dendrohyrax* as from *Procavia* and that one can differentiate three groups in the Hyracoidea no matter on which taxonomical level. Unless further studies, for example, genetic analyses, provide other evidence, I suggest that Hahn's (1935, 1959) and Bothma's (1966) recognition of three genera in the Order Hyracoidea should be retained.

ACKNOWLEDGMENTS

I would like to express my gratitude to the Tanzania National Parks Trustees, the Serengeti Research Institute, and the Ngorongoro Conservation Authorities for all their kind support; to Prof. J. Jacobs and Prof. W. Wickler for their valuable help and

advice. Many thanks also to Mr. P. Fox for his cooperation, to Mr. C. Nyaale Gagah for helping observe *D. arboreus*, and to Mrs. P. Rechten for revising the English.

Serengeti Research Institute Publication No. 220.

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PATTERNS OF SPECIATION IN AFRICAN MAMMALS

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ABSTRACT

The distribution and speciation of African mammals can be interpreted in terms of both isolation and dispersal associated with Quaternary climatic and vegetational changes. Patterns of faunal diversity and endemism suggest the former existence of refugia in Forest Regions and dispersal between these Regions. Isolation has also been significant in savanna, but dispersal patterns are less easily assessed here. In certain superspecies, the directions involved in dispersals can be ascertained from the

distribution of primitive and derivative character states, which in turn imply the cotemporal existence of ancestral and descendant taxa. Long term "ecological translation" in speciation appears to have occurred down the faunal diversity gradient, especially across the forest-savanna boundary, but also from savanna to arid zones. Different mammalian taxa have speciated in different ways and there are other impediments to the reconstruction of speciation patterns.

INTRODUCTION

Currently much attention is focusing on the historical geography and speciation of tropical biota. This paper, based on the literature and on my own taxonomic and faunistic studies mostly still in progress, draws attention to some of the main problems involved in assessing the speciation of African mammals during the fluctuating climatic conditions of the Quaternary.

The study of mammalian speciation seeks to describe the dispersion and geographic variation of species accurately, to identify hybrid zones and other types of apparent secondary contact, and to

recognize primitive and derivative characters in the species being studied. It then attempts to infer localities of refugia occupied under adverse climatic conditions and to identify directions taken during periods of dispersal. It may be possible to provide a relative chronology of events (Table 7); hypotheses of this kind gain conviction if several mammals appear to have had similar histories. Finally, it may be possible to provide more absolute chronologies, with the assistance of other disciplines, and to trace the histories of regional faunas. Many difficulties are involved in this exercise.

TERMINOLOGY

Superspecies are "monophyletic groups of entirely or essentially allopatric species too different to be included in a single species" (Mayr, 1963:44). In the plural, the term is used (Bigalke, 1972) to embrace "monospecific" superspecies as well. Allospecies are species which are members of superspecies. Semispecies are either highly distinctive subspecies or full spe-

cies whose status is debatable. Species groups are monophyletic assemblages of closely allied or sibling species, some of which may be allopatric, so that the term superspecies is inappropriate (Hall and Moreau, 1970). Subspecies groups are monophyletic groups of subspecies, which may approach species status.

SPECIATION AND ZOOGEOGRAPHY

Previous Studies

Interest in the evolutionary geography of African mammals dates from the early part of this century, with the publication of general interpretations of present faunal distributions in terms of Tertiary and Quaternary phenomena (Schwarz, 1924, 1926a; Lonnberg, 1929; Braestrup, 1935) and evolutionary studies on particular taxa, including the African buffalo, *Syncerus caffer* (Christy, 1924a, 1924b, 1929; Malbrant, 1935), monkeys, *Cercopithecus* and *Colobus* (Schwarz, 1926b, 1928, 1929), sun-

squirrels, *Heliosciurus* (Ingoldby, 1927) and hartebeest, *Alcelaphus* (Ruxton and Schwarz, 1929). Two of these papers (Schwarz, 1928; Ruxton and Schwarz, 1929) were presented as the first parts of a series on the speciation of African mammals, but there was no sequel and after such a promising beginning, no progress in the subject was made for 20 years. The works mentioned had so little impact that only Lonnberg's and Braestrup's gained passing mention by Moreau (1952), and none is discussed by Moreau (1963, 1966) or Hamilton (1976).

Nevertheless, Lonnberg (1929) had already proposed that Pleistocene climatic cycles, by breaking up and uniting habitat types, were important in initiating the speciation of African mammals.

It was not until after the Second World War that a gradual reawakening of interest in mammalian historical biogeography developed. Booth contributed studies on evolutionary geography of West African mammals (Booth 1954, 1958a, 1958b) and a reappraisal of Schwarz's (1928) work on speciation in the mona monkeys. Blancou (1954) and Grubb (1971) reassessed Christy's (1929) and Malbrant's (1935) contributions on speciation in the African buffalo. Brain and Meester (1964) analyzed speciation in southern African *Myosorex*, Groves (1971) the evolutionary dispersal of the gorilla, and Dieterlen (1971) speciation of *Dendromus*. Jotterand (1972), following the work of Matthey, discussed chromosome evolution in relation to the speciation of *Mus*. Eisentraut (1973) investigated the Pleistocene history of Fernando Po and the Cameroon highlands. Most recently, Kingdon (1971, 1974a, 1974b) has presented hypotheses to account for patterns of speciation in many African mammalian taxa.

Much important taxonomic and faunistic work continues to appear, of course, but the opportunity for adopting an evolutionary outlook does not always arise.

Speciation and Quaternary Climatic Changes

The concept that animal distribution and speciation in Africa have been strongly influenced by cycles of arid and moist climatic phases has become well established, with the work of Moreau (1952, 1963, 1966), Carcasson (1964), and other non-mammalogists. Hamilton (1976) has reviewed the evidence for climatic change implicit in the present geography of forest biota, whereas Livingstone (1975) has covered the geological and palynological evidence; the phenomenon of climatic change is well documented for Quaternary Africa, though only the more recent events can be reliably dated. We have emerged from a relatively short moist phase, dating back 10,000–12,000 years BP; prior to this there was a longer dry episode commencing at least 22,000 years BP. The periodicity of earlier paleoclimatic episodes is still uncertain, but cycles of moist and arid phases are presumed to have succeeded each other throughout the Pleistocene. These cycles led to contraction and expansion, disruption and fusion of the major vegetation zones.

Table 1.—Incidence of allospecies and superspecies in mammalian taxa in Africa.

Taxa	No. of species	No. of super-species	No. and proportion of species which are allospecies	Species/super-species ratio
Carnivores	70–76	59	24–33 (0.34–0.43)	1.2–1.3
Artiodactyls	85–96	64	36–52 (0.42–0.54)	1.3–1.5
All ungulates	95–112	72	39–63 (0.41–0.56)	1.4–1.7
Primates	45–69	30	25–49 (0.56–0.71)	1.5–2.3
Squirrels	37	26	17 (0.46)	1.3

Mammal populations associated with a particular vegetation type were thus restrained from dispersing at one period and perhaps even restricted to small refugia, yet were free to disperse at other times and invade adjacent expanding ex-refugia coalescing with their own.

Ideally, the most complete form of speciation is for one species to evolve into two sympatric species. Climatic change in Africa and the response of mammal populations facilitated the isolation and dispersion necessary for this to occur. During the isolation phase, regional differentiation was emphasized and potential mechanisms of reproductive isolation developed, whereas in the expansive phase, sympatry with former conspecifics was acquired. However, the expansive phases also provided the potential for producing further isolates, through the extension of distribution into what would become refugia once again in the next phase of the climatic cycle. Expansive phases were longest for eurytopic species, which may have continued to disperse without check, but shortest for stenotopic species differentiating in isolation. Expansive and isolating phases may have been antitemporal in forest and nonforest species, moist phases producing continuous forest, disrupting savanna, and dry phases the reverse (maps in Carcasson 1964 and Hamilton 1976).

It is difficult to believe that selection remained uniform during these cycles and it is tempting to speculate that the expansive phase was a time of more rapid phenetic change in populations at the dispersive front, which were increasing in numbers, encountering new habitats and establishing an ecological niche that had been locally unoccupied. In other words, it may be possible to regard the expansive phase, rather than the geographic disruption of populations, as the initiating element in speciation—that speciation occurs not so much by the

Table 2.—Secondary contact between species and well-differentiated subspecies.

1. Secondary intergradation: hybrids or intermediates known
 - (a) *Rhylocyon cirnei*, *R. petersi*, Tanzania (Kingdon, 1974a, but not Corbet and Hanks, 1968)
 - (b) *Paraxerus cepapi*, *P. palliatus*, Tanzania (Kingdon, 1974b)
 - (c) *Cercopithecus (aethiops) tantalus*, *C. (a.) pygerythrus*, Uganda (Dandelot, 1959)
 - (d) *Cercopithecus (mitis) mitis*, *C. (n.) Albogularis*, (Booth, 1968)
 - (e) *Cercopithecus erythrotis*, *C. cephus*, Cameroon (Struhsaker, 1970)
 - (f) *Papio anubis*, *P. cynocephalus*, Kenya (Maples, 1972)
 - (g) *Papio cynocephalus*, *P. ursinus*, Zambia and Malawi (Freedman, 1963)
 - (h) *Papio anubis*, *P. hamadryas*, Ethiopia (Gabow, 1975, and references therein)
 - (i) *Genetta tigrina*, *G. rubiginosa* (that is, *pardina*?), Natal (Pringle, 1977)
 - (j) *Dendrohyrax dorsalis*, *D. arboreus*, Uganda (Kingdon, 1971)
 - (k) *Giraffa camelopardalis reticulata*, *G. c. tipplekirchi*, Kenya (Stott, 1959)
 - (l) *Kobus (ellipsiprymnus) defassa*, *K. (e.) ellipsiprymnus*, Kenya (Backhaus, 1958)
 - (m) *Alcelaphus (buselaphus) lelwel*, *A. (b.) tora* subsp., *cokeri* in Kenya, *tora*, along Sudan-Ethiopian border (Ruxton and Schwarz, 1929)
 - (n) *A. (b.) major*, *A. (b.) lelwel*, Central African Empire (Malbrant, 1952)
 - (o) *Syncerus (caffer) nanus*, *S. (c.) caffer*, Zaire (Grubb, 1971)
 - (p) *Loxodonta (africana) cyclotis*, *L. (a.) africana*, Uganda (Bere, 1962; Laws et al., 1975)
2. Allopecies or semispecies potentially in contact, but no hybrids, intermediates or localized sympatry known

Funisciurus pyrrhopus, *F. substriatus*, Ghana

Paraxerus vexillarius, *P. byatti*, Tanzania

Paraxerus ochraceus, *P. cepapi*, Tanzania

Heliosciurus gambianus, *H. mutabilis*, Tanzania

Xerus inauris, *X. princeps*, South West Africa

Manis gigantea, *M. temminckii*, Zaire, Central African Empire?

Arctocebus calabarensis, *A. aureus*, Cameroon

Galago senegalensis, *G. inustus*, Zaire

Cercopithecus cephus, *C. ascanius*, Congo

Cercopithecus erythrogaster, *C. erythrotis*, Nigeria

Cercopithecus pogonias, *C. denti*, Zaire

Cercocebus torquatus, *C. agilis*, Rio Muni and Gabon

Papio papio, *P. anubis*, Guinea

Mandrillus sphinx, *M. leucophaeus*, Cameroon

Potamochoerus (porcus) porcus, *P. (p.) larvatus*, Zaire

Cephalophus ogilbyi, *C. callipygus*, Cameroon; Gabon

Cephalophus nigrifrons, *C. natalensis*, Kenya

Cephalophus nigrifrons, *C. rufilatus*, Zaire

Madoqua saltiana, *M. piacentinii*, Somalia

Gazella soemmerringi, *G. granti*, Ethiopia

Gazella dorcas, *G. speki*, Somalia

Alcelaphus lichtensteini, *A. buselaphus*, Tanzania

Tragelaphus (scriptus) scriptus and *T. (s.) sylvaticus*, Sudan

Table 2.—Continued.

3. Marginal sympatry
 - (a) *Elephantulus rufescens*, *E. revoili*, Somalia (Corbet and Hanks, 1968)
 - (b) *Elephantulus brachyrhynchus*, *E. fuscus*, Mozambique (Corbet 1974)
 - (c) *Cercopithecus nictitans* and *C. mitis*, Zaire (Schouteden, 1944–1946)
 - (d) *Cercopithecus mona* and *C. pogonias*, Cameroon (Schwarz, 1928; Struhsaker, 1970, records hybrids)
 - (e) *Cercopithecus mona* and *C. campbelli*, Ghana (Booth, 1955)
 - (f) *Colobus guereza* and *C. angolensis*, Zaire (Schwarz, 1929; Schouteden, 1944–1946)
 - (g) *Colobus guereza* and *C. satanas*, Cameroun (Schwarz, 1929)
 - (h) *Helogale hirtula*, *H. parvula*, Somalia (Azzaroli and Simonetta, 1966)
 - (i) *Herpestes ochraceus*, *H. sanguineus*, Somalia (Azzaroli and Simonetta, 1966)
 - (j) *Genetta angolensis*, *G. (genetta) felina*, Angola (Cabral, 1969)
 - (k) *Madoqua guentheri*, *M. kirkii*, Kenya (Hollister, 1924)
 - (l) *Redunca redunca*, *R. arundinum*, Tanzania (Vesey-Fitzgerald, 1964)
 - (m) *Gerbilurus vallinus* species-group, South West Africa (Schlitter, 1973)
 - (n) *Aethomys namaquensis*, *A. granti*, South Africa (Davis, 1974)
 - (o) *Mus mahomet*, *M. proconodon*, Ethiopia (Yalden et al., 1976)

break up of a continuous distribution, else there would be a tendency for distributions to get smaller and smaller, but by dispersal and then isolation of ancestor and “dispersate.” Chains of primitive-derivative allopecies (Table 6) can be interpreted through this hypothesis. More stable populations, away from the dispersal front, may have been more subject to a stabilizing selection.

The model discussed so far may apply to the speciation of certain mammals, yet it is not easy to arrange case histories in a sequence representing earlier and later stages of the process, because of “taxon effects” and because of the inadequacy of our data.

Speciation Patterns in Different Mammalian Taxa

The mammalian orders in Africa differ in species dispersion and interspecific relations, suggesting different modal forms of speciation.

African carnivores are ecologically tolerant and broadly distributed; only seven of 21 forest species are confined to a single Forest Region, only eight of 25 savanna species to a single Savanna Zone.

Thirteen species extend outside the continent, another five are essentially non-African, and six occur widely in both forest and savanna. There are relatively few allospecies (Table 1), although six species can be regarded as very highly differentiated vicariants of tropical Asiatic carnivores. Ungulates are not so widespread. Fifteen of 31 forest species are found in a single Forest Region, 24 of 39 savanna species are restricted to a single savanna zone. Six are essentially non-African; no chiefly African species extends outside the continent. Ungulates show a greater tendency to form superspecies and, in addition to the figures given (Table 1), there are another 16 to 20 species showing very strong geographic variation, which are hence incipient superspecies (there are only one or two cases like this in the carnivores). Except for *Papio hamadryas* in Arabia, no primate or squirrel ranges outside Africa. Primates are even more restricted in distribution; even with a conservative classification, 20 of 34 forest species are found in a single Forest Region. They also show a still stronger tendency to form superspecies. This is not merely because they are predominantly forest animals, more subjected to isolation and differentiation, for even among forest mammals they show an unusual tendency to break up into discrete taxa, to form montane subspecies, and to show complex patterns of dispersive semispeciation (Table 8). Although squirrels have the same superspecies to species ratio as carnivores, very few species are widely distributed—23 of 29 forest species are confined to single Forest Regions—and some speciation has been rather localized, evidently without repeated dispersions throughout the forest biome. There are at least four sibling species-pairs in *Funisciurus* and *Paraxerus*, so that sympatric species are more alike and more closely allied than some allospecies; the *cepapi-palliatu*s group of *Paraxerus* probably constitutes a “ring species.” Species in many genera of other small mammals also form superspecies (for example, the *Tatera afra* group, Davis, 1966). Bigalke (1972) indeed has classified all African mammals into superspecies and his figures give 1.4, 1.1, and 1.4 species per superspecies for shrews, bats, and rodents, respectively. However, in these groups generally, even more than in the particular case of squirrels, there is such frequent sympatry between similar or sibling species (for example, *Lemniscomys striatus* and *L. macculus*) that the superspecies concept is inadequate on its own. Many genera can reasonably be classified into “species groups,”

(Hall and Moreau, 1970) when a superspecies classification is not appropriate. Species of the genus *Arvicanthis* provide a good example.

Contact between species thus ranges from allopatric to sympatric and involves varying degrees of genetic introgression. With African mammals, however, very few cases of hybrid zones and related phenomena of secondary contact have been adequately described, and many are known only from brief notes or locality records on museum specimen labels. Less than 20 examples of secondary contact between semispecies and allospecies of the “larger” mammals are on record (Table 2); most are among the primates and artiodactyls, the taxa most prone to form superspecies, and the majority are in eastern Africa, along or to the east of the Western Rift. Examples f,h,i,l,m and o involve narrow hybrid zones; b,c and k concern broad zones of genetic introgression; in d,e and j, only a few hybrids are on record, and the other cases are not clear. There are at least 20 additional species-pairs, which are parapatric yet not separated by a major river barrier, where neither intermediate specimens nor localized co-occurrence are (yet) known. In a number of examples, notably monkeys along the lower Congo (Schouteden, 1944), allospecies are separated by major rivers, and in even more cases, semispecies do not even come close enough to make contact. Thus, although there are indications that contact between essentially allopatric populations involves a range from a considerable amount of gene exchange to none at all, the vast majority of relationships between allospecies and semispecies of the larger mammals—and there are more than 100 such relationships—requires evaluation in order to assess where they lie within this range. The formal taxonomy of these mammals implies a level of biological knowledge that has simply not been attained.

Among the “smaller” mammals, no hybrid zones have yet been discovered in Africa; a few cases of rather narrow sympatry between nearest-allied species are known (Table 2). The relatively large number of genera apparently with sympatric siblings includes *Crocidura*, *Epomophorus*, *Nycteris*, *Rhinolophus*, *Pipistrellus*, *Eptesicus*, *Glauconycteris*, *Scotophilus*, *Miniopterus*, *Tadarida*, *Funisciurus*, *Paraxerus*, *Graphiurus*, *Tatera*, *Dendromus*, *Malacomys*, *Aethomys*, *Lemniscomys*, *Arvicanthis*, *Praomys*, and *Mus*.

In summary, the following taxonomic differences in speciation appear to exist. Carnivores are broad-



Fig. 1.—Faunistic divisions of the Forest Biome in Africa, with presumed major Refugia (of more extreme arid phases) stippled; minor and more recent Refugia of less extreme arid phases probably occurred in intervening zones. W = Western Region, bounded by Dahomey Gap; WC = West Central Region, bounded by Oubangui-Congo Rivers, S = Sanaga River, O = Ogoou River, marking off subdivisions of the Region; EC = East Central Region, bounded by Congo River; SC = South Central Region; E = Eastern Region, boundaries only indicated, the forest itself restricted to many small riverain, mountain, and coastal "forest islands."

ly distributed so they rarely have the opportunity to form isolates and allospecies, hence they speciate less frequently. Primates and ungulates commence speciation more frequently but are not equally able to complete its later stages so as to acquire sympatry. When they do, it is only after repeated phases of isolation and dispersion, hence the existence of hybrid zones involving different levels of genetic isolation. These mammals could also evolve within the superspecies by elimination and replacement of allospecies without new sympatry being acquired (see Martin, 1972). Rodents and other small mammals speciate fast, and isolates readily become sympatric. Few chains of allopatric allospecies develop and a single sequence of isolation and dispersal can lead to speciation. Sibling sym-

patric species are not uncommon, but hybrid zones may be few. Evolution of chromosomes has been conspicuously important in developing mechanisms of reproductive isolation (see, for example, Jotterand, 1972).

Isolation in the Speciation of Forest Mammals

Based on geographical variation in its fauna, the lowland forest zone of Africa can be divided into a number of Regions (Misonne, 1963:87-88; Rahm, 1965, 1966, 1972), parts of some having presumptively been refuges for their fauna in past arid periods (Booth, 1958a: 59; Kingdon, 1971:65). Today these refuge areas are both foci of higher precipitation and centers where the regional fauna is rich-

Table 3.—Numbers of superspecies including semispecies of "larger" mammals in presumed Refuges of major Forest Regions, and in minor Regions.

Refuges and regions	Total super-species	En-demic super-species	Total species	En-demic species
Western Refuge	58	7	58	23
West-Central Refuge	68	10	69	17
East-Central Refuge	71	12	71	16
South-Central Region	51	4	51	11
Eastern Region	29	4	34	23

est. The terminology of Regions and Refuges has not been standardized and is cumbersome, so I propose a simplified set of names (Fig. 1).

In discussing the numerical strength of the regional fauna (Tables 3, 4), the shrews, bats, and muroid rodents are omitted, as their species limits and distribution are less completely known. The remaining "larger" mammals of the forest constitute 165 species and semispecies in 103 superspecies. Only eight superspecies occur wholly outside the former major refugia (Western, West-Central, and East-Central)—*Allenopithecus nigroviridis*, *Cephalophus adersi*, and six squirrels, for which the term superspecies when applicable implies a younger evolutionary unit than in other orders. The number of species occurring outside the major refugia is 39 (24% of total), or 49 (30%) if isolates from the Mt. Cameroon and Ogooué subregions are considered. This distribution pattern of superspecies and species is not inconsistent with Booth's (1958a) view that a severe Quaternary arid phase restricted the distribution of the forest fauna almost entirely to the major refugia and that a subsequent moist phase led to its dispersal and then the differentiation of derivative subspecies, semispecies and, at least in squirrels, species, outside the principal refugia as a consequence of a later and less severe arid period (ca. 22,000 years BP?). This derivative component of the forest fauna is distributed principally in the South-Central and Eastern Forest Regions.

The forest faunas decline in diversity towards the periphery of the Regions (Booth, 1958a, for the Western and West-Central faunas; Misonne, 1963, and Kingdon, 1971, for the East-Central and Eastern fauna). Endemics of different Regions overlap in distribution as well, but the overlap zones lie outside the principal refugia (Booth, 1958a, for the Western and West-Central faunas; Kingdon, 1971, for the East-Central and Eastern faunas, of his

Table 4.—Numbers of species of "larger" mammals in Forest Regions and numbers shared with other Regions.

Forest Regions	West-ern	West-Cen-tral	East-Cen-tral	South-Cen-tral	East-ern
Western	58	44	33	26	8
West-Central	44	69	50	27	9
East-Central	33	50	71	39	10
South-Central	26	27	39	51	10
Eastern	8	9	10	10	34

"northern" and "southern" forests and dispersal routes). It has been customary to make faunal zones strictly allopatric, but evidently they can also be treated cartographically as overlapping entities.

Each Forest Region shares more species with the nearest and fewer with more distant Regions (Table 4), except for the major discontinuity between the East-Central and Eastern Regions. The Western Region has a relatively high level of endemism (40%, Table 3) compared with any of the Central Regions, though collectively their level of endemism is similar (38%). Presumably this reflects the greater continuity of the Central Regions and the separation of the two major forest blocks by the Volta-Niger interfluvial area, and within it the Dahomey Gap (Booth, 1958a).

The presence of strongly marked endemic subspecies, allospecies, and full species north of the Sanaga around Mt. Cameroon, and again around the Ogooué valley to the south (Table 5), both areas lying outside the Refuge itself and having a depleted complement of the West-Central fauna, suggests a relatively complex history for this major Region. In a few instances, taxa in these separated subregions have a special affinity with each other. Thus, the monkey *Cercopithecus cephus* is replaced north of the Sanaga by *C. erythrotis*, yet populations of *C. cephus* transitional towards *C. erythrotis* (*C.c. cephodes*) occur far to the south, around the Ogooué delta. Some of the unique elements in the Mt. Cameroon area reflect probable faunal traffic with the East-Central and Western Regions, avoiding most of the West-Central Region itself; others may have diverged in subsidiary refuges adjacent to the West-Central Refuge.

The relatively impoverished (Misonne, 1963) South-Central Region shares more species with the East rather than the West-Central zones, the lower Congo acting as a barrier. It also has few endemic superspecies, implying a derivative origin of its fau-

Table 5.—Vicariants, endemics, and localized species in the West-Central Forest Region.

Genera	North of Sanaga	Sanaga to Ogooué	Ogooué Basin and South
<i>Galago</i>	<i>e. pallidus</i>	<i>e. elegantulus</i>	<i>e. elegantulus</i>
<i>Arctocebus</i>	<i>calabarensis</i>	<i>aureus</i>	—
<i>Cercopithecus</i>	<i>erythrotis</i>	<i>c. cephus</i>	<i>c. cephalodes</i>
<i>Cercopithecus</i>	<i>mona</i> and <i>p. pogonias</i>	<i>p. grayi</i>	<i>p. nigripes</i>
<i>Cercopithecus</i>	<i>n. martinii</i>	<i>n. nictitans</i>	<i>n. nictitans</i>
<i>Cercopithecus</i>	<i>preussi</i>	—	—
<i>Miopithecus</i>	—	<i>talapoin</i>	<i>talapoin</i>
<i>Mandrillus</i>	<i>leucophaeus</i>	<i>sphinx</i>	—
<i>Colobus</i>	<i>badius preussi</i>	—	—
<i>Colobus</i>	—	<i>satanas</i>	—
<i>Heliosciurus</i>	<i>rufobrachium</i>	<i>rufobrachium</i>	<i>gambianus</i>
<i>Epixerus</i>	—	<i>wilsoni</i>	<i>wilsoni</i>
<i>Paraxerus</i>	<i>cooperi</i>	—	—
<i>Funisciurus</i>	<i>isabella</i> only	<i>isabella</i> and <i>lemniscatus</i>	<i>lemniscatus</i> only
<i>Funisciurus</i>	—	—	<i>duchaillui</i>
<i>Funisciurus</i>	<i>p. raptorum</i>	<i>p. pyrrhopus</i>	<i>p. pyrrhopus</i>
<i>Genetta</i>	<i>cristata</i>	<i>servalina</i>	<i>servalina</i>
<i>Hylochoerus</i>	—	<i>meinertzhageni</i>	—
<i>Cephalophus</i>	—	<i>leucogaster</i>	<i>leucogaster</i>
<i>Cephalophus</i>	—	<i>nigrifrons</i>	<i>nigrifrons</i>
<i>Cephalophus</i>	<i>o. ogilbyi</i>	<i>callipygus</i>	<i>o. crusalbum</i>
<i>Neotragus</i>	<i>batesi</i>	<i>batesi</i>	—
<i>Tragelaphus</i>	—	<i>eurycerus</i>	<i>eurycerus</i>

na. There are a few species in the forests of north-west Angola not found in the Cuvette Centrale, which appear to have crossed the lower Congo rapids (*Funisciurus pyrrhopus*, *Lophuromys sikapusi*, *Anomalurus beecrofti*, *Miopithecus talapoin*, *Crossarchus ansorgei*, perhaps *Protoxerus stangeri loandae*), whereas *Funisciurus congicus* appears to have had a similar dispersal but has extended eastward as well, perhaps giving rise to the sibling *F. interior*.

The Eastern Forest Region corresponds to Kingdon's (1971) Southern Forest with its fauna dispersed along a "southern" route. It is actually an archipelago of montane and lowland, mainly coastal, forest. No single refugium could have existed in the Region during arid periods and there have been many opportunities for isolation and speciation. At least four superspecies are represented by two or more allospecies and several allospecies are very localized. Of the Region's 29 superspecies, 20 are found in every one of the other Forest Regions and only four are endemic. Though so poorly represented at this level, the Western Region's proportion of endemic species and semispecies is quite exceptionally high (65% of total), even though its species diversity is rather low. Hence we may presume that only widely dispersing superspecies have

been able to reach this area, and relatively recently too, and that the area is a faunal sink.

A few essentially forest mammals such as *Colobus guereza* are distributed outside the major refugia or the other regions discussed so far, and must have diverged, initially at least, in forest galleries.

Dispersal in the Forest Biome

Some indication of dispersal routes within the forest can be obtained from distribution patterns. For instance, species with highly discontinuous distributions, such as *Anomalurus pusillus*, could have dispersed through areas presently occupied by more eurytopic forest species with more continuous distributions (for example, *Heliosciurus rufobrachium*) when gradients in forest type (Hall and Swaine, 1976) were differently distributed during pluvials (Livingstone, 1975), providing a more continuous suitable environment. Other dispersal trends between the forest zones are implicit in the degree of affinity of their faunas. But certain distributions suggest there has been dispersal between the Western and East-Central Regions, avoiding the West-Central Refuge but involving Mt. Cameroon and probably following a path north of the present northern limits of the forest. The presence of *Rhinolophus macclaudi* and *Micropotamogale lamottei*

in the Western Refuge and of *R. ruwenzorii* and *M. ruwenzorii* in the highlands of the East-Central Refuge suggests one such ancient faunal continuity. More recent may be the dispersal, which accounts for the discontinuous distribution of certain montane mammals of the Cameroon and East-Central highlands. Groves (1971:49) has hypothesized that from a montane origin in the Albertine Rift highlands, the gorilla dispersed from east to west, Schaller (1963:29) believed that this dispersal was along a route north of the Uele River. Mona monkeys, mangabeys, red colobus, black and white colobus, and a squirrel (Table 8) are other species, which appear to have adopted this dispersal route and the same may explain discontinuous distributions of other forest mammals in the Central forest Regions (Misonne, 1963:87).

Dispersal of Montane Mammals

Montane mammal faunas in Africa still require adequate definition but do appear to be depauperate and hence derived. They show a strong degree of endemism, so that dispersal patterns are difficult to assess (Corbet and Yalden, 1972, and Yalden et al., 1976 for the Ethiopian Highlands; Rahm, 1965, and Kingdon, 1971, 1974a, 1974b for the Albertine Rift; Moreau, 1966, for distribution of montane "islands"). Distributions in East Africa are not inconsistent with Kingdon's (1971) concept of northern and southern dispersal routes. Recent dispersal between East Africa and the Ethiopian highlands has involved few species (*Lophuromys flavopunctatus*, *Otomys typus*, *Crocidura fumosa*, *Reduca fulvorufula*). The remarkable affinity between East African and Cameroon highland faunas is greater (*Myosorex* species, *Otomys tropicalis*, *Deudromus mesomelas*, *Cercopithecus lhoesti-preussi* super-species, *Reduca fulvorufula*, and *Paraxerus cooperi* with *Funisciurus carruthersi*, if Kingdon, 1974b, should prove correct in regarding them as allospecies). Carcasson (1964), Moreau (1966), and Coetzee and Van Zinderen Bakker (1970) tried to explain analagous distributions in butterflies and birds by erecting a pluvial montane-forest bridge across central Africa, and were followed by Eisentraut (1973). However, montane forest did not even descend to the foot of East African mountains (Livingstone, 1975) let alone spread across the continent. It is more likely that, as Livingstone proposes, floristic changes in forest type concomitant with climatic changes created suitable transitory habitats for these mammals so that in cooler paleoclimatic phases,

Table 6.—Ancestor-descendant chains of subspecies or species, based on primitive and derived characters.

1. Forest mammals; for key to symbols, see Fig. 1
 - (a) *Cercopithecus (mitis) mitis* (EC, SC) → *C. (m.) albogularis* (E)
 - (b) *Cercopithecus ascanius schmidtii* (EC) → *C. a. whitesidei*, *ascanius* etc (SC); *C. cephus cephus* (WC) → *C. c. cephalodes* (WC) → *C. erythrotis* (WC); *C. petaurista buttikoferi* (W) → *C. p. petaurista* (W)
 - (c) *Cercopithecus campbelli* (W) → *C. mona* (Volta to Sanaga) → *C. denti* (EC) → *C. wolffi* (SC); *C. pogonias grayi* (WC) → *C. p. pogonias*, *nigripes* (WC)
 - (d) *Cercopithecus preussi* (WC) → *C. lhoesti* (EC)
 - (e) *Cercocebus agilis* (EC, WC) → *C. atys atys* (W) → *C. a. lunulatus* (W) → *C. torquatus* (WC)
 - (f) *Colobus verus* (W) → *C. (badius) fove* (EC) → *C. (b.) badius* (WC)
 - (g) *Colobus satanas* (WC) → *C. angolensis* (EC, SC) → *C. polykomos polykomos* (W) → *C. p. vellerosus* (W) → *C. guereza* (N. forest border to Ethiopia, Tanzania)
 - (h) *Philantomba maxwelli* (W) → *P. monticola* (C, E)
 - (i) *Cephalophus spadix* (E) → *C. silvicultor* (W, C)
 - (j) *Neotragus pygmaeus* (W) → *N. batesi* (WC, EC) → *N. moschatus moschatus* (E) → *N. m. livingstonianus* (E)
2. Savanna and forest/savanna mammals; SS = Southern Savanna, NS = Northern Savanna, SA = Somali Arid, SWA = Southwest Arid
 - (a) *Cercopithecus (aethiops) pygerythrus* → *C. (a.) aethiops* → *C. (a.) sabaeus*
 - (b) *Papio cynocephalus* (SS) → *P. anubis* (NS) → *P. ursinus* (SWA); *P. papio* (NS) → *P. hamadryas* (SA)
 - (c) *Xerus erythropus* (NS) → *X. inauris*, *X. princeps* (SWA)
 - (d) *Cricetomys emini* (forest) → *C. gambianus ansorgei* (SS) → *C. g. gambianus* (NS)
 - (e) *Procavia habessinica* and other northern *Procavia* spp. → *P. capensis*, *P. welwitschii* (SWA)
 - (f) *Tragelaphus scriptus scriptus* (forest) → *T. s. ornatus* (SS) → *T. s. sylvaticus* (SS)
 - (g) *Taurotragus derbianus* (NS) → *T. oryx* (SS)
 - (h) *Syncerus caffer nanus* (forest) → *S. c. brachyceros* (NS) → *S. c. caffer* (NS, SS)
 - (i) *Damaliscus korrigum* (NS), *D. lunatus* (SS) → *D. dorcas* (SS)
 - (j) *Alcelaphus buselaphus tora*, *swaynei* (SA) → *A. b. cokei* (SA) → *A. b. buselaphus* (N. Africa) → *A. b. major* (NS) → *A. b. lelwel* (NS) → *A. b. caama* (SWA)
 - (k) *Madoqua saltiana* (SA) → *M. kirkii* (SA, SWA) → *M. guentheri* (SA)
 - (l) *Gazella soemmerringi* (SA) → *G. granti* (SA)
 - (m) *Equus grevyi* (SA) → *E. zebra* (SWA) → *E. burchelli* (SS) → *E. quagga* (SS)

es, montane forest or, for that matter, non-forest biota may have dispersed into lowland environments more than at present. This happens today to some extent, as some highland forest species pen-

Table 7.—*Hypothetical sequence of events in the speciation of Colobus monkeys.*

1. Dry Phase—*Colobus verus* in (West) Africa.
2. Moist Phase—*C. verus* disperses to Central Africa.
3. Dry—*C. (badius) foae* differentiates in E.C. refuge; acquires reddish pelage, greater sexual dimorphism; cephalic hair whorls diverge and are reduced.
4. Moist—*C. (b.) foai* disperses to West Africa.
5. Dry—*C. (b.) badius* differentiates in W. refuge; acquires blacker pelage, cephalic hair whorls lost.
6. Moist—*C. (b.) badius* disperses eastward to W.C. Forest Region.
7. Dry—*C. satanas* differentiates in W.C. Refuge; loses red pelage, acquires enlarged larynx, long mantle, pallid juvenile pelage (?).
8. Moist—*C. satanas* disperses to C. Regions.
9. Dry—*C. angolensis* differentiates in C. Regions; acquires white pelage, loses sexual swellings, becomes more tolerant of dry forest.
10. Moist—*C. angolensis* disperses to W. Region along route north of present forest boundary.
11. Dry—*C. polykomos* differentiates in W. Refuge—during an extreme dry period?
12. Moist—*C. polykomos* disperses eastward, principally along forest galleries.
13. Dry—*C. guereza* diverges in isolation as even more a species of dry forest (see Clutton-Brock, 1974).
14. Moist—*C. guereza* disperses widely into East Africa and Ethiopia during period which leads to present day.

strate low latitude lowland forest (*Cercopithecus hamlyni* and *C. lhoesti* itself, Rahm, 1970) and other highland species descend to lowland forest at higher latitudes (Brain and Meester, 1964, for *Myosorex*, and Misonne, 1963, for *Otomys*).

Dispersal Direction

The direction of dispersal along a particular route is more difficult to assess than the route itself and inferences can be drawn only from the general faunistic premise that small faunas, especially if they lack endemics, are derivatives of larger ones, and from the study of primitive and derivative character states of species and subspecies. In a number of forest mammals, especially the primates, it is possible to identify sequences of successively more derivative subspecies or species, suggesting that a population has dispersed and formed a new isolate, which has itself given rise to another and so on, with each climatic cycle, so that a chain of ancestors and descendants are formed, which are yet contemporaries (Table 6). Schwarz's conclusions (1926b, 1928, 1929) were similar, though he did not always distinguish primitive and derived character states.

From Table 6 it is possible to interpret the speciation of colobus monkeys in terms of seven chief dispersals between the Western and Central Forest Regions in association with seven phases of isolation and differentiation (Table 7). The last putative eastward dispersal of colobus and the succeeding phase of isolation (commencing *ca.* 35,000 years BP?) can readily be related to inferred eastward dispersal in some other monkeys and a squirrel (Table 8). The hypothesis is based on Table 6 with extrapolation to other species where primitive-derivative character states are not yet identified, and is supported by certain zoogeographical details—for instance, none of the eastward-invasive animals have managed to reach Fernando Po, whereas the "resident" species are well represented there.

Booth (1958b) interpreted these sequences in Table 8 as "stepped clines" reflecting the breakup of more continuous populations in a series of Pleistocene refugia, of which he recognized two in the Western Forest Region to account for primate subspeciation there. He did not explain how the eastern subspecies are in some cases intermediate between the western one and derivative taxa occurring outside the Region (Table 6: b,e,g). A succession of isolations and dispersals provides, I think, a better explanation.

This hypothesis can be correlated with others concerning approximately contemporaneous evolutionary events—namely the derivation of the South-Central Forest Zone primates, speciation among West-Central Forest mammals (Table 5), or the concept of a dispersal corridor between Western and Central Forest north of present forest limits—to provide a preliminary reconstruction of recent forest faunistic history. Nevertheless, the level of supposition in the reconstruction remains very apparent.

Ecological Translation across the Forest-savanna Boundary

Direction in dispersal and speciation may be considered not only in a strictly geographic sense, but also from the ecological aspect. Most African mammals are probably confined to a major biome—forest, mesic savanna, arid savanna, or desert—though the extent to which this is true has not been critically examined (see distribution maps in Smithers, 1971; Schouteden, 1944–1946; Davis, 1974). The boundary between forest and savanna is a particularly clear one, and few species occur unequivocally in both habitats even though forest species

Table 8.—Suggested eastward dispersal of western forest monkeys and a squirrel.

Genera	Primary Western Refuge	→	Secondary Refuge	→	Nigeria, W of Niger River	→	West- Central Region	→	East- Central Region	→	South- Central Region
<i>Colobus</i>	<i>p. polykomos</i>		<i>p. vellerosus</i>		<i>p. vellerosus</i>		<i>guereza</i>		<i>guereza</i>		
<i>Cercocebus</i>	<i>a. atys</i>		<i>a. lunulatus</i>		<i>torquatus</i>		<i>torquatus</i>				
<i>Cercopithecus</i>	<i>d. diana</i>		<i>d. roloway</i>								
<i>Cercopithecus</i>	<i>p. butikoferi</i>		<i>p. petaurista</i>		<i>erythrogaster</i>						
<i>Cercopithecus</i>	<i>c. campbelli</i>		<i>c. lowei</i>		<i>mona</i>		<i>mona</i>		<i>denti</i>		<i>wolffi</i>
<i>Colobus</i>	<i>b. badius</i>		<i>b. waldroni</i>				<i>b. preussi</i>				
<i>Funisciurus</i>	<i>lemniscatus</i>		<i>lemniscatus</i>		<i>raptorum</i>		<i>raptorum</i>		<i>akka</i>		
<i>pyrrhopus</i>	group		group		group		group		group		
<i>Cercopithecus</i>	<i>nictitans</i>										
	<i>stampflii</i>										
<i>Colobus</i>	<i>verus</i>		<i>verus</i>				<i>verus</i>				

penetrate savanna along forest galleries and savanna species enter the forest when it is opened up by farms and roads (Rahm, 1972).

Successively stronger levels of differentiation between forest and savanna vicariants can be recognized in at least 30 superspecies and species-groups (Table 9). Leaving these species aside, there are still at least 26 genera, which include both forest and savanna species. When the distribution and taxonomy of these animals are better known, it will probably be possible to segregate some further evolutionary units as species groups or superspecies here as well. Five families whose species have not yet been considered, and another nine which already have, contain separate forest and savanna genera. A total of 28 families occurs in both biomes, as compared with three in the forest alone and 15, of which eight are rodents, only outside the forest.

The taxonomic levels of differentiation between forest and savanna mammals suggest there has been a long-term exchange between the faunas of the biomes through infraspecific dispersal from one to the other and eventually through speciation of vicariant populations, because eurytopic species occurring in both habitats are few.

Hypothetically, faunal exchange between biomes could be equally balanced, but the evidence, such as it is, suggests that it has been predominantly from forest to savanna.

Schwarz (1924) and Lonnberg (1929) believed that plains mammals had a forest origin, and Lonnberg indeed supposed that some of the savanna mammals of Africa had originated from the stranding of forest species during a long-term recession of the Great Hylea. Understandably, this explanation was rejected by Chapin (1932) and Moreau (1952)

but its supporting evidence was not reinterpreted by either. Forest origins have been proposed or implied by various authors for Soricidae (Heim de Balsac and Lamotte, 1956, 1957), Cercopithecidae (Lonnberg, 1929; Napier, 1970), Procaviidae and Sciuridae (Lonnberg, 1929), Giraffidae (Harris, 1976), Bovidae (Estes, 1974), Nycteridae (Braestrup, 1935; Koopman, 1975), and Hystricidae (Kingdon, 1974b), while the most derived species in several of these families and in Manidae, Hippopotamidae, Suidae, Herpestinae (see Pocock, 1919; Taylor, 1974, 1976), and Felidae are clearly savanna taxa. These citations do not in themselves contribute evidence for a forest-savanna ecological translation, because the literature is diffuse and diverse, few authors having even considered the hypothesis' plausibility. The shortage of pan-African taxonomic studies and more especially of evolutionary studies partly explains this deficiency.

For families other than those mentioned above, no statement of forest origin has been made, nor can the original biome be regarded as self-evident, even though as in the case of the Pteropodidae, one is inclined to suspect it on zoogeographic grounds. Moreover, some mammalian families (for example, Gerbillidae) have had a very long history of speciation in non-forest environments and may have originated there so that their ultimate ancestral habitat cannot readily be determined. Forest origins are accepted in interpreting the phylogeny of horse, elephant, or man, but proposals for forest origins in African mammals have not all remained undisputed. Thus, Kingdon (1971) regards the forest habitat as secondary in hyraxes, not noting contrary evidence presented by Lonnberg (1929) for a forest origin, and Lonnberg himself had to make a forest

Table 9.—Mammalian taxa occurring in both forest and savanna.

1. Species with weakly differentiated forest and savanna populations
<i>Crocidura occidentalis</i>
<i>Taplozous mauritianus</i>
<i>Hipposideros conmerisoni</i>
<i>Pipistrellus nanus</i>
<i>Heliosciurus gambianus</i>
<i>Mellivora capensis</i>
<i>Lutra maculicollis</i>
<i>Genetta pardina</i>
<i>Viverra civetta</i>
<i>Atilax paludinosus</i>
<i>Panthera pardus</i>
<i>Tragelaphus spekii</i>
2. Species with strongly differentiated forest and savanna subspecies
<i>Funisciurus congicus</i>
<i>Orycteropus afer</i>
<i>Loxodonta africana</i>
<i>Potamochoerus porcus</i>
<i>Tragelaphus scriptus</i>
<i>Syncerus caffer</i>
3. Superspecies with forest (listed first) and savanna allospecies
<i>Tadarida congica</i> , <i>T. trevori</i>
<i>Manis gigantea</i> , <i>M. temmincki</i>
<i>Aonyx congicus</i> , <i>A. capensis</i>
<i>Galago inustus</i> , <i>G. senegalensis</i>
<i>Paraxerus palliatus</i> , <i>P. cepapi</i> , <i>P. ochraceus</i>
<i>Cricetomys emini</i> , <i>C. gambianus</i>
<i>Manis gigantea</i> , <i>M. temmincki</i>
<i>Aonyx congicus</i> , <i>A. capensis</i>
4. Species groups with forest and savanna allospecies
<i>Hipposideros ruber</i> , <i>H. cafer</i>
<i>Rhinolophus alcyone</i> , <i>R. landeri</i>
<i>Heliosciurus gambianus</i> , <i>H. mutabilis</i> , <i>H. rufobrachium</i>
<i>Thamnomys rutilans</i> , <i>T. cometes</i> , <i>T. dolichurus</i>
<i>Lemniscomys</i> species-complex
5. Genera with separate forest and savanna species
(a) Species additional to those already listed in the following genera
<i>Crocidura</i> , <i>Taplozous</i> , <i>Hipposideros</i> , <i>Pipistrellus</i> , <i>Rhinolophus</i> , <i>Galago</i> , <i>Genetta</i> , <i>Tragelaphus</i>
(b) Species in the following genera
<i>Sylvisorex</i> , <i>Epomops</i> , <i>Rousettus</i> , <i>Nycteris</i> , <i>Eptesicus</i> , <i>Glauconycteris</i> , <i>Scotophilus</i> , <i>Kerivoula</i> , <i>Myopterus</i> , <i>Tadarida</i> , <i>Cercopithecus</i> , <i>Deudromus</i> , <i>Aethomys</i> , <i>Praomys</i> , <i>Graphiurus</i> , <i>Bdeogale</i> , <i>Felis</i>
6. Families with different forest and savanna genera
Soricidae, Macroscelididae, Cercopithecidae, Pteropodidae, Sciuridae, Cricetomyidae, Muridae, including <i>Oenomys</i> - <i>Thamnomys</i> group, <i>Malacomys</i> group, <i>Acomys</i> group and <i>Arvicanthis</i> group, Procaviidae, Hystricidae, Hippopotamidae, Suidae, Giraffidae, Viverridae, Bovidae

habitat secondary for bovids, because he was mistakenly forced to believe that they had radiated outside the continent. Kortland's dehumanization hypothesis suggests a savanna origin for the chimpanzee (Kortland and Kooij, 1963; Kortland and Van Zon, 1968); Buettner-Janusch (1966:267) proposed a forest invasion by *Cercopithecus*; and Kingdon's (1971) speculation on *Galago* required speciation out of, but then back into, the forest. Misonne (1969) considers murids to be primarily savanna animals in Africa, yet he regards forest as a marginal refuge habitat (1969:167, 171) for certain more primitive species. From his conclusions, it seems quite possible that apart from the *Praomys* and *Mus* groups, all African murids could represent a single radiation within the Continent; there seems to be no very compelling reason for supposing that the occurrence of certain primitive genera and species in the forest should not indicate a forest origin for this radiation.

Few other statements to the effect that African forest mammals were derived from savanna species have been made. The problem of ultimate biome origin is nevertheless not an easy one to handle, for speciation across a major ecotone can be interpreted in several ways from primitive-derivative characters. With a colonist in biome B and its cotemporal primitive ancestor in biome A, there has been a dispersive speciation from A to B, but, if the ancestor is itself replaced in A by a third and even more advanced form, while the taxon in B retains primitive features, dispersal could be misinterpreted as having occurred from B to A. Animals like *Sylvicapra grimmia* and *Cercopithecus aethiops*, for example, retain very conservative color patterns and hair-banding characters, with respect to their congeners in the ancestral forest habitat, yet a wealth of evidence suggests that ecological drift in Bovidae and Cercopithecidae has indeed been from forest to savanna.

Evidence for relatively recent dispersal into the savanna by forest mammals comes from a study of certain eurytopic species or species groups occurring in both biomes. These mammals exhibit a morphological continuum between populations, yet have areas of parapatry, sympatry, or secondary intergradation between extreme phenotypes where demes have converged on each other in dispersing from different areas. Primitive characters occur in the forest populations, more derivative ones in the savanna, whereas the reverse is not usually evident.

The buffalo, *Syncerus caffer*, provides one of the best examples (Grubb, 1971, and in preparation), so great is the contrast between the forest and savanna forms and so clear are the derivative characters of the latter. This species and the elephant, *Loxodonta africana*, apparently dispersed into the savanna in West Africa and continued their dispersal through the Northern Savanna and around the forest block into Angola and South Africa. In East Africa, both replaced other species in the late Pleistocene—the more primitive *Homoioceros* and the more derivative *Elephas recki* (Maglio, 1973).

More species appear to have crossed the southern forest-savanna border, and in Angola there is clinal variation between forest and savanna populations of *Hipposideros* (*caffer* group, Koopman, 1975), *Cricetomys*, and *Heliosciurus*, which in other parts of Africa are sympatric. The *Hipposideros caffer* group, the giant rat *Cricetomys*, the bushbuck, *Tragelaphus scriptus*, and the bushpig, *Potamochoerus percus*, all have dispersed from the forest through the Southern Savanna northward into East Africa. The bushbuck did not reach farther than southern Sudan in this northward progression, other subspecies having colonized Ethiopia and the Northern Savanna, but the bushpig did get to the Ethiopian highlands. *Cricetomys gambianus* and *Hipposideros caffer* have spread farther, throughout the Northern Savanna, the latter coexisting with its forest congener *H. ruber* where this species penetrates savanna.

A third route has been adopted by the squirrel *Funisciurus congicus*. Species of this genus reach into the savanna along riverain forest (*F. pyrrolopus*, *F. anerythrus*, *F. substriatus*, *F. bayoni*) but *F. congicus* extends much further, from the forest of the Cuvette Central south through western Angola into the dry mopane woodland of South West Africa, in one continuous clinal sequence.

Speciation and Dispersal in Savanna and Arid Biomes

Endemism or vicariantism of non-forest mammals tends to be related to the two Savanna Zones or three Arid Zones of Davis (1962) with, for instance, *Taurotragus derbianus* in the Northern Savanna, *T. oryx* in the Southern, or *Oryx dammah* in the Sudanese, *O. beisa* in the Somali, *O. gazella* in the South West Arid (Ansell, 1972). These Zones have hence been centers of isolation, but it is unlikely that they were ever reduced to small refugia, contra Moreau (1966:98).

Other regions have had a less prominent role in speciation. In the Northern Savanna, a number of endemics are found only east (for example, *Hologale dybowskii*) or west (for example, *Genetta thierrii*) of the Lake Chad and Chari Basin area, whereas certain taxa are represented by divergent allospecies or subspecies in these regions (Schwarz, 1926a; Grubb, 1971; Groves, 1975). The Pleistocene lake Megachad may have been the instrumental barrier to dispersal here. A small faunal element is located in the Senegal area, including endemic semispecies (particularly *Papio papio* and *Sylvicapra grimmia coronata*) and isolates of otherwise widely distributed species. The factor encouraging isolation is not known. The Nile swamps and Ethiopian Highlands were probably also refuge centers for savanna mammals in arid periods.

In the Southern Savanna, the Muchinga scarp is involved in separating semispecies of baboons, blue monkeys, sun-squirrels, and waterbuck (Ansell, 1960) and may have accounted for speciation between roan and sable antelopes, for it lies central to their area of sympatry. The Rufiji basin (Kingdon, 1974a) and the Escarpment Zone of Angola (Cabral, 1966) have also been proposed as barriers promoting isolation in mammals, whereas others such as the Nyasa Rift were probably involved. Endemism in southern Africa is discussed by Rautenbach (1978) and speciation in *Elephantulus*, *Otomys*, and *Chrysochloridae*, for example, must have been complex in this part of the Continent. Speciation in Saharan mammals, particularly rodents, is perhaps best linked with evolutionary studies of the whole Eremian fauna. There is a complex situation in the Somali Arid Zone, with speciation or secondary contact among large- and small-nosed dikdik, giraffe, larger and smaller gazelles, hartebeest, and zebras (Keast, 1965). The mammals making up the famous East African Plains Fauna, which occurs within the Zone, are of diverse zoogeographical affinity and wildebeest, gazelle, and perhaps hartebeest and rhinoceros (see Brooks, 1961; Groves, 1967) have been influenced in their subspeciation by the Kenya Rift. The discontinuous distribution of species and superspecies in the Somali and South West Arid zones has been extensively discussed and explained by dispersal along a former Arid Corridor during a dry climatic phase (Benson and White, 1960; Ansell et al., 1962; Ansell, 1960; Bigalke, 1972). The dry-savanna mammals of the Rukwa valley and isolated populations of wildebeest, giraffe, and tsessebe in Zambia (An-

sell, 1960) perhaps represent a vestige of this dispersal.

Dispersal directions are not always easily inferred in non-forest mammals but they may have involved complex patterns of replacement with very wideranging dispersal. For example, in their northern distributions, as well as in southern Africa, neither hartebeest nor baboons have their most closely allied allospecies in contact. The Ethiopian hartebeest, *tora*, is phylogenetically nearer the West African *major* or the extinct North African *buselaphus* than the very different Sudanese *lelwel* with which it forms a hybrid zone (Ruxton and Schwarz, 1929). And *Papio papio* of Gambia and Senegal is nearer *P. hamadryas* of Ethiopia and Somalia than *P. anubis* of the intervening Northern Savanna (Hill, 1970).

A notable problem is the absence of any indication of dispersal through Angola and Congo to the Central African Empire, where a route should have been available when forest was reduced to small refugia (see Carcasson, 1964; Hamilton, 1976). The significance of this has yet to be assessed.

A number of superspecies are not restricted to arid or savanna zones, but show more complex distribution patterns, with some allospecies in both mesic and arid zones and others in only one or the other. This group includes mammals where the Northern Savanna form is either restricted to the Guinea Savanna or is more eurytopic, reaching into the Sudanese Arid Zone, whereas the nearest ally is a stenotopic Southern Arid species. *Alcelaphus (buselaphus) lelwel*, *Papio anubis*, *Xerus erythropus*, and *Procapra latastei* in the Northern Savanna are represented by *A. (b.) caama*, *P. ursinus*, *X. inauris*, and *P. capensis* in the Southern Arid Zone, to which they are restricted. Related trends are seen in *Sylvicapra grimmia*, where derivative subspecies have penetrated the Southern Arid, yet conservative subspecies have not dispersed into the Sudanese Arid (Groves, personal communication), and the eland, where the primitive *Taurotragus der-*

bianus is restricted to Guinea savanna, yet the derivative *T. oryx* is much more habitat-tolerant and extends into the Kalahari. The giraffe, white rhinoceros, and hedgehog are also in part more ecologically restricted in their southern distributions.

These distribution patterns suggest an ecological translation from mesic to arid habitats, a view supported by the derivative character of all the Southern Arid allospecies (Table 6). Other Southern Arid or Grassland species (*Oryx gazella*, *Antidorcas marsupialis*, *Damaliscus dorcas*, *Connochaetes gnou*, *Phacochoerus aethiopicus aethiopicus*, *Equus quagga*) are also derivative. And the paucity and strongly derivative adaptations of desert mammals suggest that they too have originated from other habitats.

Ecological Direction in Dispersive Speciation

From this discussion and earlier remarks about forest origins of savanna species, it would appear that if speciation involves an ecological translation from one biome to another, then it is predominantly from mesic, predictable and less seasonal habitats toward arid, less predictable and more seasonal environments, and hence involves a descent of the species-diversity gradient. The slope of this gradient in Africa is considerable; it is best measured in areas where habitats are clearly stratified, as in West Africa. Rosevear (1949) presents data from which it can be calculated. The gradient in number of mammal species per biome is 130, 60, 47, 37 from forest through Guinea, Sudan, and Sahel savannas in Nigeria. These data are provisional; I obtain 141, 106, 86, 49 and 22 (desert) for the same transect west of the Volta River. Implications for theories of faunal steady states (MacArthur, 1972:174; Rozennweig, 1975), or faunal exchange (Wilson, 1965) arise if dispersive speciation is indeed predominantly unidirectional along this gradient, and the possibility that biomes are faunistically imbalanced necessarily follows.

CONCLUSION

An important impediment to the reconstruction of speciation in African mammals is the scarcity of taxa with apparently significant and interpretable geographic variation and dispersion. It is impossible to recognize centers of dispersal or refugia when variation is clinal and low-key, and it is impossible

to trace any dispersal track when primitive-derivative characters have not been recognized. And these may be misleading, in suggesting a dispersal direction opposite to the one which occurred. There is in any case some danger in assuming that primitive-derivative morphological series always repre-

sent ancestors and descendants, though this may be nearer the truth and at least no more mistaken than suggesting that two contemporaries share an extinct common ancestor that was phenetically equidistant between them. However, in many cases, the temporal divergence in morphology that does occur between primitive and derivative stocks once gene flow between them has ceased must now obscure the relationship.

Very few reconstructions of species histories are likely to be possible, therefore, even with the degree of surmise entailed in the *Colobus* model (Table 7). The absolute time span involved in a case like this is hard to assess, for we do not know what scale of paleoclimatic events were needed to drive the isolation-dispersal system, and therefore whether speciation took a longer or shorter time. Even relative time-scaling presents problems. Taxa that have diverged to different degrees, for instance, may have speciated at different rates or over different periods of time, and there may now be no

way of distinguishing such equally parsimonious hypotheses. Even with a single superspecies, events may get telescoped—a succession of divergences may be regarded as cotemporal (Booth, 1958b).

What we clearly need are more evolutionary data for developing more rigorous models of speciation. We may expect further paleontological studies to do this for the larger mammals and karyological work for the smaller species, as it has already contributed so much outside Africa. Logistic problems may allow faunistic and taxonomic studies to hold sway for some time and we certainly need many more accurate distribution maps. The classification of distributions is an important first step in reconstructing faunal histories. Some of the hypotheses presented in this paper are supported by evidence from African birds, reptiles, and butterflies and a less sectarian approach may in the future prove more productive.

ACKNOWLEDGMENTS

I am grateful to the American Philosophical Society, the Royal Society, the Carnegie Museum of Natural History and the Uni-

versity of Ghana for grant support or for financial assistance in attending the Colloquium.

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THE DAHOMEY GAP—A REEVALUATION OF ITS SIGNIFICANCE AS A FAUNAL BARRIER TO WEST AFRICAN HIGH FOREST MAMMALS

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ABSTRACT

The Dahomey Gap as a faunal barrier to high forest mammals is reevaluated. Past researchers, utilizing incorrect or incomplete data, were led to the conclusion that the Gap was the major factor influencing high forest animal distribution in West Africa. Recent data on climate, vegetation, soil type, and mammalian

taxonomy, ecology, and distribution indicate that the Dahomey Gap has not influenced mammal distribution or evolutionary changes. Rather, it is the Volta and Niger rivers, which have affected mammalian distribution and speciation in West Africa.

INTRODUCTION

The Dahomey Gap, as an ecogeographical barrier to high forest animals, has been discussed by many authors including Booth (1954, 1958a, 1958b) and Dekeyser (1955) for mammals, Clausen (1964) for fishes, Schiotz (1967) for tree frogs, and Moreau (1969) in his synopsis of the origin and effects of this barrier. Mammals collected recently from isolated patches of high forest within the Gap suggested that there was no barrier. Prior to this analysis the only faunal data available were from the forests bordering the western and eastern limits of the Gap.

The collections (1967–1968) of mammals made by the Smithsonian African Mammal Project under the direction of H. W. Setzer, from the forest of southeastern Ghana, the forest of southwestern Nigeria, and particularly the southern parts of Togo and Dahomey (=Benin) (see Robbins, 1978, for Togo and Dahomey bats); and collections in Togo by the Laboratoire de Zoologie du Rijksuniversitair Centrum van Antwerpen in conjunction with the Musée Royal de l'Afrique Centrale (in Tervuren, Belgium) (for additional Togo bats see DeVree, DeRoo, and Verheyen, 1969; DeVree, Hulselmans, and Verheyen, 1970; and DeVree and Van der Straeten, 1971), provide new information on the ecogeographical significance of the Dahomey Gap.

The presence of high forest mammals within the Dahomey Gap necessitates a reevaluation of the following points.

1) On vegetation maps of Africa, a prominent feature is the division of the evergreen forests of West Africa into eastern and western parts—the Upper Guinea Forest (Guinea Forest block), which extends from the Volta River in Ghana west to Guinea, and the Lower Guinea Forest (Congo For-

est block), which extends from southwestern Nigeria, across southern Nigeria, and east to Gabon and Zaire. The area between is commonly known as the Dahomey Gap (Moreau, 1969). The so-called Dahomey Gap is therefore an irregular area which takes in the southern parts of Togo and Dahomey, and southeastern Ghana (Clausen, 1964). Fig. 1 shows the major vegetation zones in the area under consideration in this report.

2) Within the Gap the savanna vegetation, which characterizes the West African interior, extends south to the Gulf of Guinea (Clausen, 1964).

3) The southern parts of the Gap, especially in Togo and Ghana, are in fact amazingly arid, generally resembling the Sudan Savanna in climate and vegetation (Clausen, 1964).

4) About half of the width of the Gap is occupied by a forest-savanna mosaic in the form of a strip bordering each forest block. Within this mosaic the forest patches are evidently small today. The central 100 mi of the Gap is a humid savanna (Moreau, 1969).

5) Some descriptions (Dekeyser, 1955; Booth, 1958b) claim that the Gap could be defined as a forest relict and may not be a formidable barrier. Moreau (1969) suggests that this may refer to the zone between the Volta River and the Togo highlands as having forest patches.

6) For forest animals the Dahomey Gap would be expected to form an important barrier that would result in evolutionary divergence at its two edges (Moreau, 1969).

7) Moreau (1969) reported that Schiotz (1967) found no forest animals in the forest patches within the Gap.

8) The limits of the forest and the forest-savanna

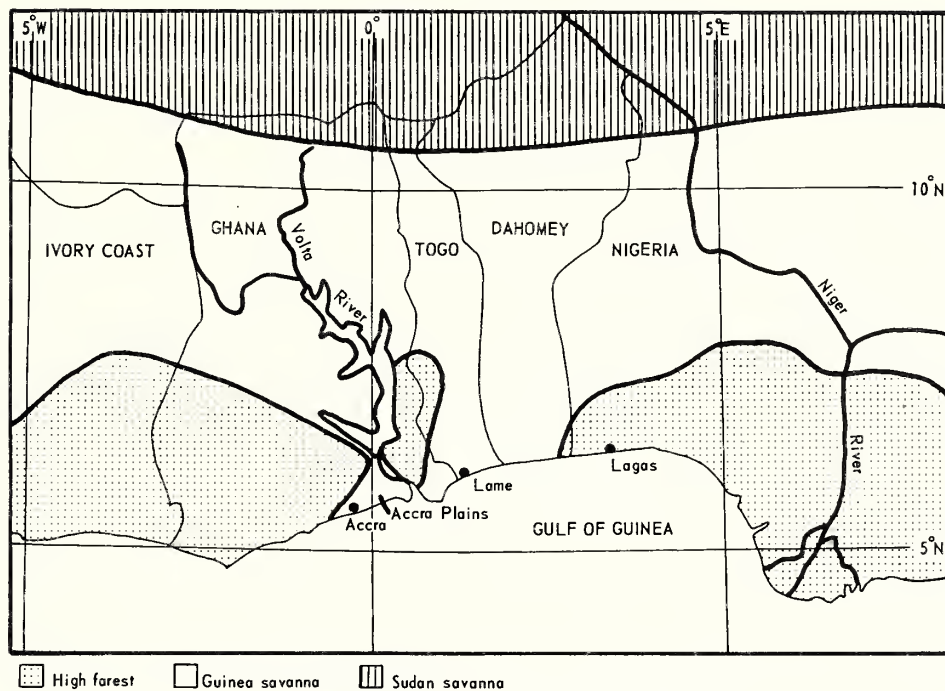


Fig. 1.—Major vegetation zones in West Africa.

mosaic do not seem to conform closely to the rainfall isohyets (Moreau, 1969).

9) The mammal distribution data examined by Booth (1958*b*) suggested to him that the Niger and the Volta rivers form the most important zoogeographical barriers in present-day West Africa. The Dahomey Gap in its present form is of less importance, but in the past must have had a considerable influence on the differentiation of the fauna east of the Niger and west of the Volta (Booth, 1958*b*).

10) A break in the forest approximating the location of the Dahomey Gap has been present for the last 10,000 years, prior to which time the Upper and Lower Guinea forests were united for at least an equal period (Moreau, 1969).

11) D. E. Livingstone (personal communication, 1977) said it was reasonable to accept the Dahomey Gap as a barrier, probably dating in its present form from about 5,000 years ago. He believes that most of that time breaks in continuous forest vegetation probably were few and of short duration until human interference changed the landscape.

12) The climatic picture is one of drought for some few thousand years prior to 12,000 BP; increased rainfall, especially between 10,000 and 5,000 BP; and a reversion to a more arid climate since about 5,000 BP (D. E. Livingstone, personal communication, 1977).

This paper presents an analysis of the effects of the Dahomey Gap based on recent climate, vegetation, soil type, and mammal distribution data. The evidence presented here contradicts the data and conclusions of Moreau (1969). He presented data, which established the Dahomey Gap as the major faunal barrier in West Africa. Apparently he drew his conclusions about 10 years too soon. Moreau (1969) admitted that his evidence was puzzling and contradictory. This may be because he used information extrapolated from East African climatic history to West Africa, which was either not pertinent or incorrect, and also before the taxonomy, distribution, and ecology of high forest animals were better known.

DISCUSSION AND RESULTS

Vegetation and Climate

Vegetation characteristics in equatorial tropical Africa are dependent on several factors. Among

these are climate and soil type. Rosevear (1965) characterizes the high forest in West Africa as a distinguishable vegetation zone requiring at least

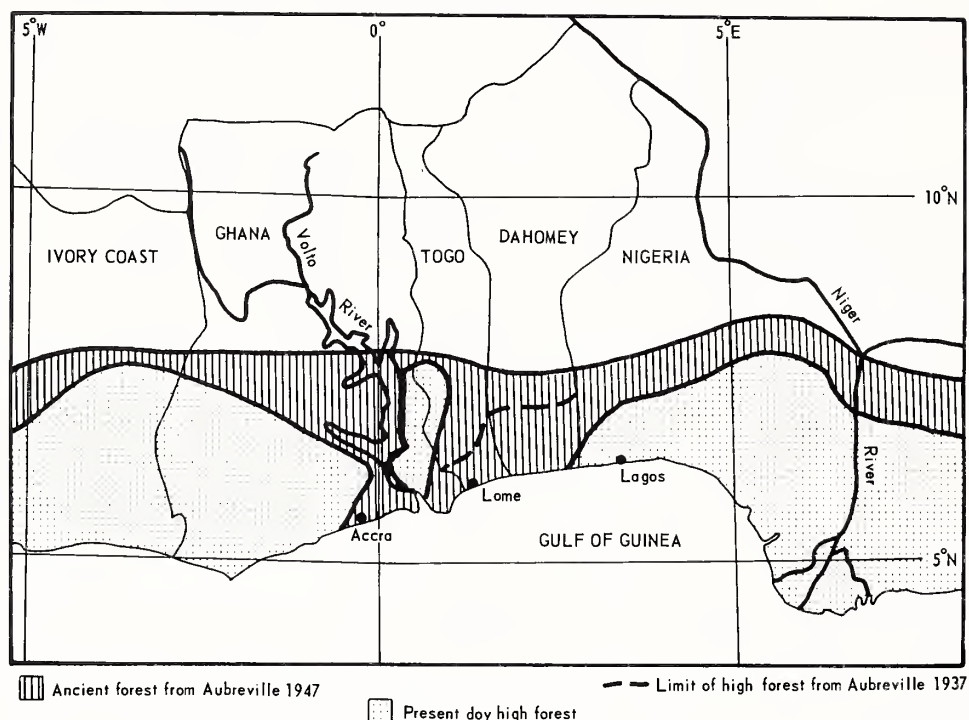


Fig. 2.—Present-day and ancient high forest zones in West Africa.

200 cm of rainfall annually. As Moreau (1969) points out, the limits of the forest do not conform closely to the rainfall isohyets. Because of this, other factors must be considered to determine the effectiveness of the annual total rainfall on the distribution of high forest vegetation. Temperature, relative humidity, air movement, soil condition, drainage, and topography are some of those factors (Richards, 1966).

One or several of these factors must be different (see Aubreville, 1949) if the climate and vegetation of the Dahomey Gap differs from the forests to the east and west, by being more arid and resembling the savanna (Clausen, 1964). Livingstone (1975) and others report climatic changes in Africa during the Quaternary. The Dahomey Gap area would have been at times a savanna bounded on both sides by high forest, at other times a part of a continuous forest, and at other times a part of a more widespread coastal savanna.

The zoogeographical data Moreau (1969) presented would seem logical if the Dahomey Gap existed in the form of a savanna for the past 10,000 years. However, following Livingstone (1975, personal communication, 1977), with a change to a more arid climate beginning about 5,000 BP, the

following statements on vegetation and mammals become more meaningful.

The forest-savanna mosaic, also termed derived savanna, contains patches of high forest vegetation not confined to streams. It is generally agreed that this zone (which includes the Dahomey Gap area) has been covered with high forest in the past (the ancient forest) and that it is the influence of man that has transformed these areas into savanna (Schiotz, 1967). The derived savanna area has microclimatic patterns characteristic of the savanna influenced by changes in the vegetation cover (Schiotz, 1967).

The first major study of high forest characteristics and origins in the Dahomey Gap area was by Aubreville (1937). That study indicated that during the early 1900's there were still vestiges of an ancient forest in Togo and Dahomey. He experienced forest clearings for agricultural purposes throughout the area. Also, he stated that if the disappearance of the forest was of an old happening, then the forest patches would be long gone. His analysis of the species composition of those forest patches indicated that they were the same as the large bordering equatorial forest blocks.

Aubreville (1937) traveled throughout the area of

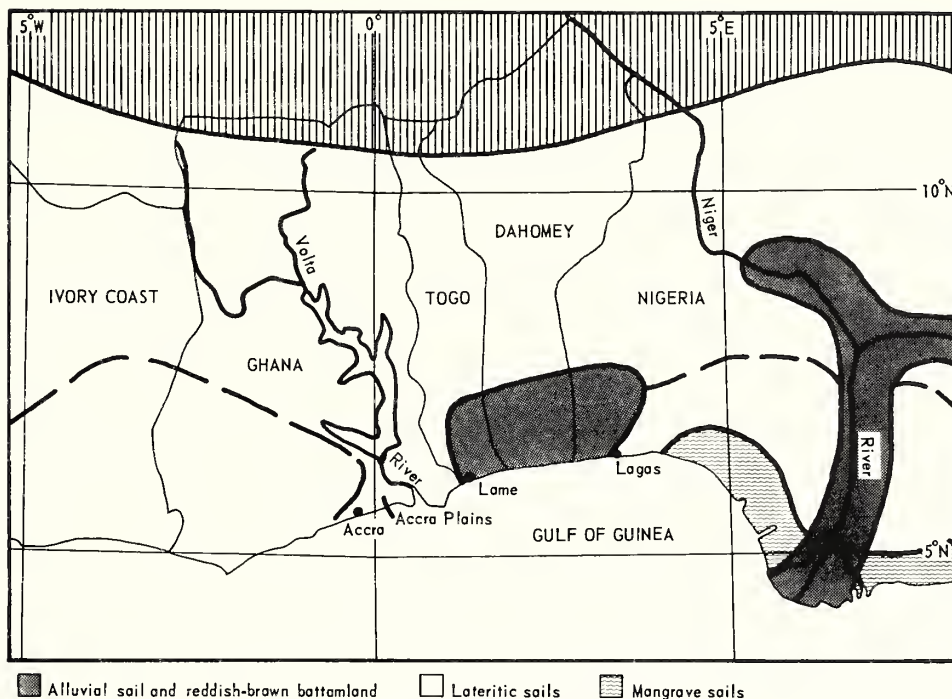


Fig. 3.—Major soil types in West Africa.

the Dahomey Gap exploring for evidence to determine the northern limit of the ancient coastal forest. He determined that it was up to 60 to 80 km from the coast in Dahomey and 40 km in Togo. In a later paper (Aubreville, 1949), the area occupied by the ancient forest was enlarged (Fig. 2). His evidence was the persistence of species of large trees known to occur only in the equatorial high forest. Although the destruction of the forest was extensive at the time of Aubreville, my examination of ERTS-1 (taken in 1973) and LANDSAT-2 (taken in 1976) satellite photographs in conjunction with first hand observations (in 1968), shows the presence of isolated patches of high forest still present within the Dahomey Gap area.

The humid tropical and equatorial high forest zones of Africa are usually characterized by lateritic soil types. The term laterite may be applied to the end result of a process, which preferentially leaches silica from the substrate. The end result is a soil having a mixture of alumina and iron oxides with very little else (Richards, 1966). Lateritic soils are also characterized by a low nutrient and organic content, with resulting low fertility. However, this soil readily supports the tropical high forest because of continuous nutrient recycling (FitzPatrick, 1971). When high forest vegetation is eliminated in agri-

cultural practices the fertility of the soil is quickly exhausted and crop failure results. This may account for the shifting of cultivated areas in high forest zones (FitzPatrick, 1971). After vegetation removal, plant succession back to the high forest community with subsequent soil nutrient regeneration, can take from 20 years to a century or more (Richards, 1966).

However, a different soil type occurs in the Dahomey Gap area between Lome, Togo, and Lagos, Nigeria. This area is composed of alluvial soils (sands) and reddish-brown bottomland (The Atlas of Africa, 1973; Fig. 3). These soils probably have a high nutrient and organic content. Climatic conditions are such that left undisturbed, this area would support typical high forest vegetation. Because of the high nutrient and organic content of the soil, continued land use for agriculture is possible after the high forest is removed. This type of continual land use would result in what Richards (1966) calls a "deflected succession." This means a shifting of the biotic climax to resemble other climatic climaxes, though not the rain forest from which they were derived (Richards, 1966). In the area of the Dahomey Gap this "deflected succession" is culminated in the replacement of the high forest by open grassland, which may be called de-

Table 1.—Mammalian taxa which occur from west of the Volta River to east of the Niger River.

<i>Scotonycteris zenkeri</i>
<i>Scotonycteris ophiodon</i>
<i>Hypsignathus monstrosus</i>
<i>Nanonycteris veldkampii</i>
<i>Myonycteris torquata</i>
<i>Megaloglossus woermanni</i>
<i>Taphozous peli</i>
<i>Nycteris grandis</i>
<i>Nycteris argae</i>
<i>Hipposideros cyclops</i>
<i>Hipposideros fuliginosus</i>
<i>Pipistrellus nanus</i>
<i>Mimetillus moloneyi</i>
<i>Chalinolobus poensis</i>
<i>Cercopithecus nictitans martini</i>
<i>Idiurus macrotis cansdalei</i>
<i>Anomalurus beecrofti</i>
<i>Anomalurus derbianus</i>
<i>Atheurus africanus</i>
<i>Hybomys univittatus</i>
<i>Lophuromys sikapusi</i>
<i>Malacomys longipes</i>
<i>Hylomyscus</i> sp.
<i>Praomys</i> sp.
<i>Thamnomys rutilans</i>
<i>Graphiurus hueti</i>
<i>Funisciurus leucogenys</i>
<i>Funisciurus substriatus</i>

rived savanna, and can be maintained as a biotic climax. This has led to recurrent statements in the literature by many authors implying that the Dahomey Gap is a natural savanna extension to the coast between two major forest blocks. In fact it is an area modified by man, which would normally be covered by high forest and is probably no older than the advent of man practicing intensive agriculture.

The limit of the Dahomey Gap given by Booth (1958b), Clausen (1964), and Moreau (1969) is between the Volta River in eastern Ghana and southwestern Nigeria. Clausen (1964) also apparently included the Accra Plains in southeastern Ghana,

Table 2.—Mammalian taxa which occur from the Volta River to the west.

<i>Hipposideros jonesi</i>
<i>Colobus waldroni</i>
<i>Colobus verus</i>
<i>Cercopithecus campbelli</i>
<i>Cercopithecus diana roloway</i>
<i>Anomalurus peli</i>
<i>Hybomys trivirgatus</i>
<i>Heliosciurus rufobrachium maculatus</i>
<i>Protoxerus aubinni</i>
<i>Epixerus ebii</i>

Table 3.—Mammalian taxa which occur from the Niger River to the east.

<i>Epomops franqueti franqueti</i>
<i>Arctocebus calabarensis</i>
<i>Galago alleni</i>
<i>Galago crassicaudatus</i>
<i>Galago demidovi murinus</i>
<i>Perodicticus potto juju</i>
<i>Cercopithecus erythrogaster</i>
<i>Potamochoerus porcus pictus</i>
<i>Dendrohyrax dorsalis nigricans</i>

which extended the Gap west of the Volta River. For the purposes of this report the Accra Plains, being a unique area vegetationally and not a part of the Lower Guinea Forest block, and because high forest vegetation and animals are found between the Volta River and continuing into the western Togo highlands, the Dahomey Gap is considered to lie between the western Togo highlands and southwestern Nigeria.

Mammalian Fauna

Many of the major vertebrate groups have been examined with reference to distribution and effects of the Dahomey Gap. Marchant (1954) examined birds; Clausen (1964) cyprinodont fishes; Schiotz (1967) tree frogs; and Booth (1954, 1958a, 1958b) primates and most other mammalian orders. These data provided the faunal information used by Moreau (1969) in his examination of the physical and ecological faunal barriers in West Africa.

Moreau (1969) chose not to supplement the above studies with other data. He believed (correctly) that compilations from general check lists with imprecise taxonomy and ecology would not be useful. His report states (p. 40) “. . . defective though the available data are, there is no doubt that in sum they provide a basis for valid discussion of an exceedingly interesting situation.”

Table 4.—Mammalian taxa which occur from the Niger River to the west.

<i>Epomops franqueti strepitans</i>
<i>Perodicticus potto potto</i>
<i>Galago demidovi demidovi</i>
<i>Colobus polykomos vellerosus</i>
<i>Cercopithecus petaurista petaurista</i>
<i>Malacomys edwardsi</i>
<i>Dendrohyrax dorsalis sylvestris</i>
<i>Potamochoerus porcus porcus</i>
<i>Cephalophus maxwelli</i>
<i>Cephalophus niger</i>

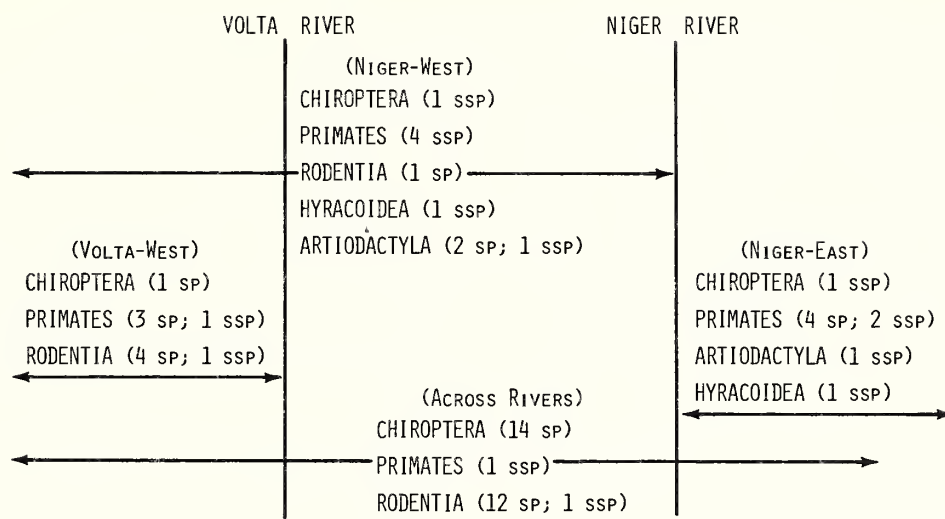


Fig. 4.—Mammalian taxa changes by order for the four major distributional categories.

One problem that becomes evident on examination of the previous reports on birds, fishes, tree frogs, and mammals, is that they were not collected within the area of the Dahomey Gap. As mentioned in the introduction, mammal specimens are now available from the Dahomey Gap as well as additional specimens from areas west and east of the Gap. Also, many of the major mammalian groups have been studied so that information on their taxonomy and ecology is available and compiled in a series edited by Meester and Setzer (1971).

Moreau (1969) discussed the influence of three topographical features as faunal boundaries—the Lower Niger River, the Dahomey Gap, and the Baoule V/Bandama River. Booth (1958b) also included the Volta River as a faunal barrier. To assess the possible influence of the Dahomey Gap on West

African high forest mammalian fauna, taxonomy and ecology of mammals occurring from Nigeria west through Ivory Coast were studied. The mammal species and/or subspecies were divided into four categories.

The categories include taxa which occur (1) across the whole area under consideration (that is, across both rivers), (2) only west of the Volta River, (3) only east of the Niger River, and (4) only west of the Niger River. Three other categories were originally considered: taxa occurring only between the two rivers; those occurring only east of the Volta River; and those occurring from the western edge of the Gap and continuing westward. High forest

Table 5.—Influence of the major river barriers.

Major river barriers	Species changes		Subspecies changes	
	N	Percent	N	Percent
Across Rivers	26	45.6	2	3.5
Volta—West	8	14.0	2	3.5
Niger—East	5	8.8	4	7.0
Niger—West	3	5.3	7	12.3
Totals	42	73.7	15	26.3
Percent of Influence				
Niger	= 33.4			
Volta	= 17.5			
Across Rivers	= 49.1			
	100.0			

Table 6.—Mammalian taxa found in the Dahomey Gap forest patches.

<i>Epomops franqueti strepitans</i>
<i>Myonycteris torquata</i>
<i>Megaloglossus woermanni</i>
<i>Hipposideros cyclops</i>
<i>Pipistrellus nanus</i>
<i>Chalinolobus poensis</i>
<i>Perodicticus potto potto</i>
<i>Galago demidovi demidovi</i>
<i>Cercopithecus petaurista petaurista</i>
<i>Cercopithecus nictitans martini</i>
<i>Cercopithecus mona</i>
<i>Protoxerus stangeri nigeriae</i>
<i>Funisciurus leucogenys</i>
<i>Funisciurus pyrrhopus nigrens</i>
<i>Lophuromys sikapusi</i>
<i>Hylomyscus</i> sp.
<i>Praomys</i> sp.
<i>Cephalophus maxwelli</i>

taxa in these latter three categories comprise only 8% of the total, so were excluded from the percent of taxa different in each of the four main categories.

Tables 1–4 list the taxa, which have been included in each of the four categories. Table 5 consolidates these four tables and gives the number of taxa in each category and percent of the total. It is divided to reflect species or subspecies change. These results are summarized in Fig. 4 with the number of taxa in each of the five mammalian orders in the four categories.

These data show that of the 57 taxa examined, 49.1% occur in both the Upper and Lower Guinea forests and their distribution is not affected by the Volta River, the Dahomey Gap, nor the Niger River. Of the remaining taxa (50.9%), 33.4% are influenced by the Niger River. The Niger seems almost equally effective in limiting distribution of mammal taxa occurring east of the river (15.8%) and those occurring west of the river (17.6%). In contrast, the Volta River primarily restricts the distribution of taxa, which occur to the west (17.5%). Of the species occurring east of the Volta only one (*Cercopithecus mona*) does not cross, whereas one has a subspecies boundary at the Volta with *Heliosciurus*

rufobrachium isabellinus occurring east of the river and *H. r. maculatus* occurring west of the river.

The Dahomey Gap forest patches contain 18 species of mammals (Table 6). Of these taxa, 10 occur across both rivers, five from the Niger to the west, two from the Volta to the east, and one occurs only between the two rivers.

It is apparent from these data that contrary to previous reports, the Dahomey Gap has had little influence as a faunal barrier on the distribution of high forest mammals in West Africa. In contrast, both the Volta and Niger rivers have been major factors influencing mammal distribution, with the Niger being the more important (33.4% as opposed to 17.5% for the Volta). It is possible that the Akosombo Dam on the Volta and the resulting large Volta Lake will further restrict distribution to the north of the dam and allow greater ease of crossing the river to the south of the dam. In any case, land use, which results in forest destruction in the Dahomey Gap area, with its different soil type, may result in a Gap, which may play an important role in future speciation and distribution of West African high forest mammals.

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A NUMERICAL RE-APPRAISAL OF THE SOUTHERN AFRICAN BIOTIC ZONES

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ABSTRACT

The acceptability and credibility of the empirically derived biotic zones of southern Africa are mathematically tested by means of Duellman's (1965) Faunal Resemblance Factor analysis. The distribution of 275 southern African mammalian species

is analyzed. A total of six biotic zones, including three that were formerly regarded as subzones, are found to be viable biogeographic entities of full zonal status.

INTRODUCTION

Zoogeography has been defined as "... the scientific study of the distribution of animals on earth ..." (Udvardy, 1969:1). Through the years a number of attempts have been made to classify animal life into meaningful distributional units, and the field has been subdivided in diverse ways toward different ends. Perhaps the suggested subdivision most pertinent to this paper is that proposed by Darlington (1957:11), who distinguishes three possible levels of approach: 1) geographical distribution over the entire earth; 2) regional distribution over selected segments of the earth; 3) local distribution, including species geography ("the geographical distribution of species in relation to each other and to ecology and evolution").

This study will consider a statistical analysis of the distributional trends of southern African mammals, in an effort to reevaluate the validity and credibility of the empirically derived biotic zones of the southern subcontinent. It is primarily aimed at the second level of Darlington's zoogeographical approach, and deals with the regional distribution of the mammals of southern Africa. Unfortunately regional studies such as this are often bound to political, rather than natural, areas.

Udvardy (1969:6) distinguishes static faunistic and regional zoogeography from dynamic causal zoogeography. He furthermore distinguishes specifically between zoogeography and ecology. Zoogeography in its purest sense concerns itself with the reasons for the arrival and settling of a species in a certain area. A study of why and how a species is able to live in that particular area is an ecological problem. Similarly, Simpson (1965:71-73) recognizes three levels of zoogeography—geographical, ecological, and historical. Both the zoogeographical and ecological attributes of distribution are the

product of evolutionary processes during the course of time; hence, truly explanatory models can only be framed on a historical basis.

An accurate and detailed knowledge of subspeciation is essential in most modern computations aimed at causal zoogeography. The reverse is, however, also true; a consideration of the biogeography of taxa is important when studying subspeciation. Zoogeography and taxonomy are thus interdependent. The subspecific status of the majority of southern African mammals is, in the modern context, unsatisfactorily resolved, and thus severely hampers any detailed and accurate biogeographical analysis. Available analytical procedures based on subspeciation have therefore not been considered in this study pending further detailed survey work and subsequent taxonomic studies on the subspecies level. Consequently, this study is essentially limited to Udvardy's static faunistic and regional zoogeographical approach, and is thus primarily ecological in context.

The major biogeographical zones or provinces currently accepted for Africa stem from Sclater (1896). He subdivided Africa into four subregions—the Sahara, West Africa, Cape, and Malagasy. Recently, the Malagasy subregion was upgraded to regional status (Darlington, 1957). Hence the current concept of the Ethiopian region is Africa south of the Sahara.

Chapin (1923, 1932), working on the avifauna of Zaire (formerly Belgian Congo), combined former approaches (Wallace, 1876; Sclater, 1896; Reichenow, 1900; Sharpe, 1893) with his own knowledge of the birds of tropical Africa. He divided Zaire into distinct avifaunal regions, which he based on vegetation types best fitting the distribution of birds. Chapin then attempted to follow these avifaunal re-

gions into adjacent countries, eventually arriving at a subdivision of the Ethiopian region into biogeographical districts. His West African subregion, as well as his East and South African subregions, correspond closely to the subregions of Sclater (1896). Both approaches were essentially aimed at a broad separation of tropical forests from savannas and deserts.

In Chapin's (1932) treatise of Africa, southern Africa was subdivided into only two faunal districts—an eastern and a western-arid district. Chapin's work was soon accepted (see Bates, 1924; Lynes, 1924). However, Chapin (1932) himself comments that the least satisfactory portion of his zoogeographical map of Africa is the southern African district. He considers further subdivision necessary here, especially in order to accommodate the highveld grassland and the woodland savanna, as well as tropical montane and coastal forests.

Moreau (1952) collates and critically discusses the Tertiary geology and climate of Africa. In this light, he analyzes the distribution of passerine avifauna of Africa, firstly by biomes, and secondly with respect to its affinities with the avifaunas of Europe and Asia. He geographically subdivides these main biomes into smaller biotic zones. He considers affinities both on generic and specific levels, and found differences between these derived biotic zones to be great.

With regard to southern Africa, Moreau (1952) retains Chapin's (1923) South West Arid district more or less unaltered, as a biotic zone. However, Moreau introduces the concept of the Southern Savanna biotic zone, which combines Chapin's eastern, climatically moderate, woodland districts. As suggested by Chapin (1932), Moreau now also recognizes montane forests as distinct on a biotic zone level. He furthermore recognizes the small, but floristically very rich and distinct winter rainfall area around Cape Town, with its Mediterranean climate, as a separate biotic zone.

Moreau (1952) uses both the terms "biotic zone" and "biome." The first term has a definite zoogeographical connotation, the second ecological. According to Smith (1966), the biotic province (zone) concept "... embraces a continuous geographic area that contains ecological associations distinguishable from those of adjacent provinces (zones), especially at the species and subspecies level. . . ." The biome, on the other hand, is a major ecosystem, and is seen by Smith as "... a broad eco-

logical unit characterized by the distinctive life forms of the climax species, plant or animal. . . ." Southern African biotic zones can in reality also be seen as biomes, except that as such they are only parts of the major biomes of Africa. Whatever the case, Moreau can be credited to be one of the first to employ the correct terminology in an African zoogeographical treatise, with consideration to concepts and terms developed in related fields such as ecology. This distinction between "biotic zone" and "biome" is recognized and applied in this report.

Davis (1962) employs the southern African portion of Moreau's (1952) biogeographical map in an analysis of distribution patterns of the local Muridae. He agrees with Moreau in the validity of the South Western Cape as a biotic zone. However, Davis' (1962) main zoogeographical contribution lies in the fact that for the first time the biotic zones, which were founded on avifaunal distributional data, are analyzed from a mammalian point of view, albeit on only one family. Davis slightly alters the borders of the biotic zones to conform with the vegetation map of Keay (1959).

In a discussion of the origins of the southern African mammalian fauna, Meester (1965) accepts Davis' modified version of Moreau's biotic zones. Although Davis' generalized attempts to subdivide the biotic zones went unnoticed, Meester's definite recognition of the Namib as a subzone of the South West Arid, and the Grassland as a subzone of the Southern Savanna, was soon accepted. This approach to the recognition of biotic zones is even more compatible with the biome concept.

There are other proposed systems for subdividing the subcontinent into major biogeographic units, especially those of Liversidge (1962) and Winterbottom (1962). However, the biotic zone concept as outlined above has become commonly accepted as relevant from an ecological viewpoint, especially with regard to higher vertebrates. It is also, to my knowledge, the only zoogeographical system considered in recent years for work on mammal distribution (see Davis, 1962; Meester, 1965). It is therefore appropriate that biotic zones should receive closer scrutiny here, especially because no less than four currently recognized major biotic zones (two with two subzones each) are represented in southern Africa. Meester's (1965) refined version of Moreau's (1952) biotic zones is analyzed in this report.

METHODS

The African biotic zones and subzones have been empirically derived by considering main vegetation types and how they best fit the distribution of species, initially of birds and later of mammals. The zones are thus largely subjective. A number of species may be confined to a single biotic zone (endemics), but very few have ranges coinciding entirely with the boundaries of the particular zone in which they occur. Generally their ranges are more restricted. Such endemic species are few in number, yet serve as the main argument to justify the recognition of the biotic zone. The majority of species occurs over several biotic zones, because the distributions are limited by factors more generalized than those governing the vegetation types on which the biotic zones are primarily based. These widespread species apparently formerly served no role in justifying the recognition of biotic zones.

Duellman (1965:677) proposes a statistical analysis to express the validity of biogeographical subdivisions, based on the known distribution of all species in the entire area. He termed it the "Faunal Resemblance Factor," which is statistically expressed as $FRF = 2C/N_1 + N_2$, where C equals the number of species in common between the two zones compared, N_1 equals the

number of species in the first zone, and N_2 equals the number of species in the second zone. An index value of 0.000 would indicate no taxonomic resemblance between two zonal faunas, and an index of 1.000 would indicate complete identity. A value of 0.500 would indicate that one-half of the species in each of the two zonal faunas are held in common, provided that they are of equal size. In the case of unequal-sized faunas, both dissimilarity in species composition and relative equality in species density are expressed. Duellman's (1965) formula is a simplified, yet equally effective, derivative of the Burt coefficient (Burt, 1958). Both formulas take the average of the two samples as the denominator (contrary to the Simpson and Jaccard coefficients, see Simpson, 1960), in an effort to reduce the effect of difference in size between them. However, the influence of differential faunal sizes is not entirely eliminated, and is yet another factor expressing similarity or dissimilarity between zones. These formulas are furthermore designed for taxa of which the geographical distributions of species are not well known. Only the presence or absence of taxa is of great importance. The Duellman coefficient is therefore ideally suited for this analysis, and was decided upon as being the simplest of the two mentioned here.

RESULTS

The distributions of 275 species of southern African mammals are given in Table 1. This list was compiled from updated but unpublished distribution maps kept in the Transvaal Museum for curatorial purposes, as well as from the literature, particularly Smithers (1971), Meester and Setzer (1971–1977), Davis (1974), Pringle (1974), Lynch (1975), and Smithers and Lobao Tello (1976). The taxonomic treatise of Meester and Setzer (1971) was followed. In the calculation of FRF indices, the Southern Savanna Grassland and Woodland subzones and the Namib subzone were treated as hypothetically valid zones, as indicated in Table 1. The list excludes feral and exotic species, as well as poorly known endemics of doubtful taxonomic status. As far as possible, the natural (historic) ranges of species were considered, thus compensating for human impact. Species with extremely limited ranges, or known from only a few localities, were considered as representative of the biotic zone in which they occur. Where the majority of localities for a species fall within a given zone, with only a few isolated instances falling just inside an adjacent zone, these were considered as typical only of the zone where the distribution is concentrated, and not as a constituent of the mammal fauna of the second zone. However, if such scattered localities are deep into

the second zone, they were considered typical of that zonal fauna as well. Judgment was subjective. Typical Forest zone species occurring outside that zone, but restricted to riverine forests, were considered as pure forest zone species. However, the influence of dispersal corridors, such as the Kuiseb and Orange rivers, was not taken into account.

The distribution of bats as a group is particularly poorly documented, which may adversely influence the results of this analysis. Excluding bats was considered. However, certain mammalian taxa, as well as nutritionally and ecologically adapted groups, demonstrate diverse latitudinal clinal trends in composition and densities (Nel, 1975). Thus it was decided to include the meager information on bats in an effort to retain a more balanced image of trends in overall mammalian ecological distribution.

A simple matrix of similarity, indicating the degree of interrelationships of mammalian faunas of southern African biotic zones, is given in Table 2. Absolute numbers of species in common are indicated below the diagonal. Italic numerals on the diagonal indicate the number of species in each zone, and the bracketed numerals underneath these denote the known number of endemic species. Above the diagonal is an index of faunal resemblance, calculated after Duellman (1965).

Table 1.—Distribution of southern African mammals according to Biotic Zones.

Taxa	Biotic Zones					
	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
<i>Petrodromus tetradactylus</i>	—	—	—	X	—	X
<i>Macroscelides proboscideus</i>	X	X	—	—	—	—
<i>Elephantulus intufi</i>	X	X	—	X	—	—
<i>Elephantulus rupestris</i>	—	X	—	—	—	—
<i>Elephantulus myurus</i>	—	—	—	X	X	—
<i>Elephantulus edwardi</i>	—	X	—	—	—	—
<i>Elephantulus brachyrhynchus</i>	—	—	—	X	X	—
<i>Erinaceus frontalis</i>	—	X	—	X	X	—
<i>Myosorex varius</i>	—	—	X	X	X	X
<i>Myosorex cafer</i>	—	—	—	X	X	X
<i>Suncus lixus</i>	—	—	—	X	—	—
<i>Suncus gracilis</i>	—	—	—	—	X	—
<i>Sylvisorex megalura</i>	—	—	—	—	—	X
<i>Crocidura occidentalis</i>	—	—	—	X	—	X
<i>Crocidura flavescens</i>	—	—	X	—	X	X
<i>Crocidura luna</i>	—	—	—	—	—	X
<i>Crocidura mariquensis</i>	—	—	—	X	X	—
<i>Crocidura hirta</i>	—	X	—	X	X	X
<i>Crocidura silacea</i>	—	—	—	X	X	X
<i>Crocidura cyanea</i>	X	X	—	X	X	X
<i>Crocidura maquassiensis</i>	—	—	—	X	X	—
<i>Crocidura bicolor</i>	—	X	—	X	—	—
<i>Chrysospalax trevelyani</i>	—	—	—	X	—	X
<i>Chrysospalax villosus</i>	—	—	—	X	X	X
<i>Cryptochloris wintoni</i>	—	X	—	—	—	—
<i>Cryptochloris zyli</i>	—	—	X	—	—	—
<i>Chrysochloris asiatica</i>	—	X	—	—	—	—
<i>Chrysochloris visagiei</i>	—	X	—	—	—	—
<i>Eremitalpa granti</i>	X	X	X	—	—	—
<i>Chlorotalpa sclateri</i>	—	X	—	—	X	—
<i>Chlorotalpa duthiae</i>	—	—	—	—	—	X
<i>Chlorotalpa arendsi</i>	—	—	—	—	—	X
<i>Galcochloris obtusirostris</i>	—	—	—	X	—	—
<i>Amblysomus gunningi</i>	—	—	—	—	—	X
<i>Amblysomus hottentotus</i>	—	—	—	X	X	X
<i>Amblysomus iris</i>	—	—	—	X	X	X
<i>Amblysomus julianae</i>	—	—	—	X	X	—
<i>Eidolon helvum</i>	—	X	—	X	X	—
<i>Epomophorus walilbergi</i>	—	—	—	X	—	X
<i>Epomophorus gambianus</i>	—	—	—	X	—	—
<i>Epomophorus crypturus</i>	—	—	—	X	—	—
<i>Epomophorus angolensis</i>	—	—	—	X	—	—
<i>Rousettus aegyptiacus</i>	—	—	—	X	—	X
<i>Rousettus angolensis</i>	—	—	—	—	—	X
<i>Taplozous mauritanus</i>	—	—	—	X	—	—
<i>Taplozous perforatus</i>	—	—	—	X	—	—
<i>Coleura afra</i>	—	—	—	X	—	—
<i>Nycteris hispida</i>	—	—	—	—	—	X
<i>Nycteris grandis</i>	—	—	—	—	—	X
<i>Nycteris macrotis</i>	—	—	—	X	—	X
<i>Nycteris woodi</i>	—	—	—	X	—	X
<i>Nycteris thebaica</i>	X	X	—	X	—	X
<i>Rhinolophus hildebrandti</i>	—	—	—	X	—	X
<i>Rhinolophus fumigatus</i>	—	X	—	X	—	—
<i>Rhinolophus clivus</i>	—	—	X	X	X	X

Table 1.—Continued.

Taxa	Biotic Zones					
	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
<i>Rhinolophus darlingi</i>	X	X	—	X	—	—
<i>Rhinolophus landeri</i>	—	—	—	X	—	—
<i>Rhinolophus blasii</i>	—	—	—	X	—	—
<i>Rhinolophus capensis</i>	—	X	X	X	—	—
<i>Rhinolophus simulador</i>	—	—	—	X	—	—
<i>Rhinolophus denti</i>	—	X	—	X	—	—
<i>Rhinolophus swinnyi</i>	—	—	—	X	—	—
<i>Hipposideros commersoni</i>	—	X	—	X	—	—
<i>Hipposideros caffer</i>	—	X	—	X	—	X
<i>Triaenops persicus</i>	—	—	—	X	—	—
<i>Cloeotis percivali</i>	—	—	—	X	—	—
<i>Myotis welwitschii</i>	—	—	—	X	X	—
<i>Myotis seabrai</i>	—	X	—	—	—	—
<i>Myotis lesueuri</i>	—	—	X	—	—	—
<i>Myotis tricolor</i>	—	X	—	X	X	—
<i>Myotis bocagei</i>	—	—	—	X	—	—
<i>Nycticeius schlieffeni</i>	—	X	—	X	—	—
<i>Pipistrellus nanus</i>	—	—	—	X	—	X
<i>Pipistrellus kuhli</i>	—	—	—	X	—	X
<i>Pipistrellus rusticus</i>	—	—	—	X	—	X
<i>Pipistrellus rueppelli</i>	—	—	—	X	—	—
<i>Eptesicus rendalli</i>	—	—	—	X	—	—
<i>Eptesicus hottentotus</i>	X	X	—	X	—	—
<i>Eptesicus melckorum</i>	—	—	X	—	—	—
<i>Eptesicus zuluensis</i>	X	X	—	X	—	—
<i>Eptesicus somalicus</i>	—	—	—	X	—	—
<i>Eptesicus capensis</i>	—	X	—	X	X	—
<i>Eptesicus notius</i>	—	—	X	—	—	—
<i>Glauconycteris variegata</i>	—	—	—	X	—	—
<i>Laephotis wintoni</i>	—	—	—	X	—	—
<i>Scotophilus gigas</i>	—	—	—	X	—	—
<i>Scotophilus nigrita</i>	—	—	—	X	—	—
<i>Scotophilus leucogaster</i>	—	X	—	X	—	—
<i>Kerivoula argentata</i>	—	—	—	X	—	—
<i>Kerivoula harrisoni</i>	—	—	—	X	—	—
<i>Kerivoula lanosa</i>	—	—	—	X	—	X
<i>Miniopterus fraterculus</i>	—	—	—	X	—	—
<i>Miniopterus schreibersi</i>	X	X	—	X	X	X
<i>Otomops martiensseni</i>	—	—	—	X	—	—
<i>Saunmys petrophilus</i>	—	X	—	X	—	—
<i>Tadarida acetabulosus</i>	—	—	—	X	—	—
<i>Tadarida midas</i>	—	X	—	X	—	—
<i>Tadarida niveiventer</i>	—	—	—	X	—	—
<i>Tadarida condylura</i>	—	—	—	X	—	X
<i>Tadarida nigeriae</i>	—	X	—	X	—	—
<i>Tadarida chapini</i>	—	—	—	X	—	—
<i>Tadarida pumila</i>	—	—	—	X	—	—
<i>Tadarida fulminans</i>	—	—	—	X	—	—
<i>Tadarida aegyptiaca</i>	—	X	X	X	X	X
<i>Tadarida ansorgei</i>	—	—	—	X	—	—
<i>Galago crassicaudatus</i>	—	—	—	X	—	X
<i>Galago senegalensis</i>	—	X	—	X	—	X
<i>Papio cynocephalus</i>	—	—	—	X	—	—
<i>Papio ursinus</i>	X	X	X	X	X	X
<i>Cercopithecus mitis</i>	—	—	—	X	—	X

Table 1.—Continued.

Taxa	Biotic Zones					
	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
<i>Cercopithecus aethiops</i>	—	X	—	X	—	X
<i>Manis temmincki</i>	—	X	—	X	X	—
<i>Otocyon megalotis</i>	—	X	—	X	—	—
<i>Vulpes chama</i>	X	X	—	X	X	—
<i>Canis mesomelas</i>	X	X	—	X	X	—
<i>Canis adustus</i>	—	—	—	X	—	—
<i>Lycaon pictus</i>	—	X	—	X	—	—
<i>Ictonyx striatus</i>	X	X	—	X	—	—
<i>Poecilogle albinucha</i>	—	X	—	X	X	—
<i>Mellivora capensis</i>	—	X	—	X	—	—
<i>Lutra maculicollis</i>	—	X	—	X	X	—
<i>Aonyx capensis</i>	—	X	—	X	X	—
<i>Nandinia binotata</i>	—	—	—	—	—	X
<i>Viverra civetta</i>	—	—	—	X	—	—
<i>Genetta genetta</i>	X	X	X	X	X	—
<i>Genetta tigrina</i>	—	—	X	X	—	X
<i>Genetta rubiginosa</i>	—	—	—	X	—	—
<i>Genetta mossambica</i>	—	—	—	X	—	—
<i>Suricata suricatta</i>	X	X	—	—	X	—
<i>Paracynictis selousi</i>	—	—	—	X	—	—
<i>Bdeogale crassicauda</i>	—	—	—	X	—	—
<i>Cynictis penicillata</i>	—	X	—	X	X	—
<i>Herpestes ichenumon</i>	—	—	—	X	—	—
<i>Herpestes pulverulentus</i>	—	X	—	—	X	—
<i>Herpestes sanguineus</i>	—	X	—	X	X	X
<i>Herpestes ratlamuchi</i>	—	X	—	X	—	—
<i>Rhynchogale melleri</i>	—	—	—	X	—	X
<i>Ichneumia albicauda</i>	—	—	—	X	—	X
<i>Atilax paludinosus</i>	—	X	X	X	X	X
<i>Mungos mungo</i>	—	X	—	X	—	—
<i>Helogale parvula</i>	—	X	—	X	—	—
<i>Proteles cristatus</i>	X	X	—	X	X	—
<i>Hyaena brunnea</i>	X	X	—	X	X	—
<i>Crocuta crocuta</i>	X	X	—	X	X	—
<i>Felis libyca</i>	X	X	X	X	X	—
<i>Felis nigripes</i>	—	X	—	—	X	—
<i>Felis serval</i>	—	—	X	X	—	—
<i>Felis caracal</i>	X	X	—	X	X	—
<i>Panthera pardus</i>	X	X	X	X	X	X
<i>Panthera leo</i>	—	X	X	X	X	—
<i>Acinonyx jubatus</i>	—	X	—	X	—	—
<i>Orycteropus afer</i>	—	X	—	X	X	—
<i>Loxodonta africana</i>	—	X	—	X	—	—
<i>Procavia capensis</i>	X	X	X	X	X	X
<i>Procavia welwitschii</i>	X	X	—	—	—	—
<i>Heterohyrax brucei</i>	—	—	—	X	—	—
<i>Dendrohyrax arboreus</i>	—	—	—	X	—	—
<i>Diceros bicornis</i>	—	X	X	X	—	—
<i>Ceratotherium simum</i>	—	X	—	X	X	—
<i>Equus zebra</i>	X	X	—	—	—	—
<i>Equus burchelli</i>	—	X	X	X	X	—
<i>Potamochoerus porcus</i>	—	—	X	X	—	X
<i>Phacochoerus aethiopicus</i>	—	X	—	X	—	—
<i>Hippopotamus amphibius</i>	—	X	X	X	X	—
<i>Giraffa camelopardalis</i>	—	X	—	X	—	—

Table 1.—Continued.

Taxa	Biotic Zones					
	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
<i>Cephalophus natalensis</i>	—	—	—	X	—	X
<i>Cephalophus monticola</i>	—	—	—	X	—	X
<i>Sylvicapra grimmia</i>	—	X	X	X	X	—
<i>Raphicerus campestris</i>	—	X	X	X	X	—
<i>Raphicerus melanotis</i>	—	—	X	X	—	—
<i>Raphicerus sharpei</i>	—	—	—	X	—	—
<i>Ourebia ourebi</i>	—	—	—	X	X	—
<i>Neotragus moschatus</i>	—	—	—	X	—	—
<i>Oreotragus oreotragus</i>	X	X	—	X	—	—
<i>Madoqua kirki</i>	—	X	—	—	—	—
<i>Pelea capreolus</i>	—	X	X	X	X	—
<i>Redunca arundinum</i>	—	—	—	X	—	—
<i>Redunca fulvorufula</i>	—	—	—	X	X	—
<i>Kobus ellipsiprymnus</i>	—	X	—	X	—	—
<i>Kobus vardonii</i>	—	—	—	X	—	—
<i>Kobus leche</i>	—	—	—	X	—	—
<i>Aepyceros melampus</i>	—	X	—	X	—	—
<i>Aepyceros petersi</i>	—	X	—	X	—	—
<i>Antidorcas marsupialis</i>	X	X	—	—	X	—
<i>Oryx gazella</i>	X	X	—	X	—	—
<i>Hippotragus leucophaeus</i>	—	—	X	—	—	—
<i>Hippotragus niger</i>	—	—	—	X	—	—
<i>Hippotragus equinus</i>	—	—	—	X	—	—
<i>Damaliscus lunatus</i>	—	—	—	X	—	—
<i>Damaliscus dorcas dorcas</i>	—	—	X	—	—	—
<i>Damaliscus dorcas phillipsi</i>	—	X	—	—	X	—
<i>Alcelaphus buselaphus</i>	—	X	—	X	X	—
<i>Alcelaphus lichtensteini</i>	—	X	—	X	—	—
<i>Connochaetes taurinus</i>	—	X	—	X	—	—
<i>Connochaetes gnou</i>	—	—	—	—	X	—
<i>Tragelaphus scriptus</i>	—	—	X	X	—	—
<i>Tragelaphus spekei</i>	—	—	—	X	—	—
<i>Tragelaphus angasi</i>	—	—	—	X	—	—
<i>Tragelaphus strepsiceros</i>	—	X	—	X	—	—
<i>Taurotragus oryx</i>	—	X	X	X	X	—
<i>Syncerus caffer</i>	—	—	—	X	—	—
<i>Lepus capensis</i>	—	X	—	X	X	—
<i>Lepus saxatilis</i>	—	X	—	X	X	—
<i>Bunolagus monticularis</i>	—	X	—	—	—	—
<i>Pronolagus crassicaudatus</i>	—	—	—	X	—	—
<i>Pronolagus rupestris</i>	—	X	—	X	X	—
<i>Pronolagus randensis</i>	—	X	—	X	X	—
<i>Bathyergus janetta</i>	—	X	—	—	—	—
<i>Bathyergus suillus</i>	—	—	X	—	—	X
<i>Georchus capensis</i>	—	X	X	—	X	—
<i>Cryptomys damarensis</i>	—	X	—	—	—	—
<i>Cryptomys hottentotus</i>	—	X	—	X	X	X
<i>Hystrix africaeaustralis</i>	X	X	—	X	X	X
<i>Petromus typicus</i>	X	X	—	—	—	—
<i>Thryonomys swinderianus</i>	—	—	—	X	—	—
<i>Thryonomys gregorianus</i>	—	—	—	X	—	—
<i>Xerus inauris</i>	—	X	—	—	X	—
<i>Xerus princeps</i>	—	X	—	—	—	—
<i>Heliosciurus rufobrachium</i>	—	—	—	X	—	X
<i>Funisciurus congicus</i>	—	X	—	—	—	—

Table 1.—Continued.

Taxa	Biotic Zones					
	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
<i>Paraxerus palliatus</i>	—	—	—	—	—	X
<i>Paraxerus cepapi</i>	—	—	—	X	—	—
<i>Pedetes capensis</i>	X	X	—	X	X	—
<i>Graphiurus ocularis</i>	—	X	X	—	—	—
<i>Graphiurus platyops</i>	—	X	—	X	X	—
<i>Graphiurus murinus</i>	—	X	—	X	X	X
<i>Cricetomys gambianus</i>	—	—	—	X	—	X
<i>Dendromus nyikae</i>	—	—	—	—	—	X
<i>Dendromus melanotis</i>	—	X	X	X	X	X
<i>Dendromus mesomelas</i>	—	—	X	X	X	X
<i>Dendromus mystacalis</i>	—	—	—	X	X	X
<i>Malacothrix typica</i>	—	X	—	—	X	—
<i>Mystromys albicaudatus</i>	—	—	X	—	X	—
<i>Petromyscus monticularis</i>	—	X	—	—	—	—
<i>Petromyscus collinus</i>	X	X	—	—	—	—
<i>Saccostomus campestris</i>	—	X	X	X	X	—
<i>Steatomys pratensis</i>	—	X	—	X	—	—
<i>Steatomys krebsi</i>	—	X	—	—	X	—
<i>Steatomys minutus</i>	—	X	—	X	X	—
<i>Acomys spinosissimus</i>	—	—	—	X	—	X
<i>Acomys subspinosus</i>	—	—	X	—	—	X
<i>Aethomys granti</i>	—	X	—	—	—	—
<i>Aethomys namaquensis</i>	X	X	X	X	X	—
<i>Aethomys chrysophilus</i>	—	X	—	X	—	—
<i>Aethomys nyikae</i>	—	—	—	X	—	—
<i>Dasyurus incomtus</i>	—	—	X	X	X	—
<i>Mus indutus</i>	—	—	—	X	X	—
<i>Mus minutoides</i>	X	X	X	X	X	X
<i>Lemniscomys griselda</i>	—	X	—	X	—	—
<i>Pelomys fallax</i>	—	—	—	X	—	X
<i>Praomys natalensis</i>	—	X	X	X	X	X
<i>Praomys shortridgei</i>	—	—	—	X	—	—
<i>Praomys verreauxi</i>	—	—	X	—	—	X
<i>Rhabdomys pumilio</i>	X	X	X	X	X	X
<i>Thallomys paedulcus</i>	X	X	—	X	—	—
<i>Thamnomys cometes</i>	—	—	—	—	—	X
<i>Thamnomys dolichurus</i>	—	—	—	X	—	X
<i>Zelotomys woosnami</i>	—	X	—	—	—	—
<i>Parotomys brantsi</i>	X	X	X	—	—	—
<i>Parotomys littledalei</i>	X	X	—	—	—	—
<i>Otomys laminatus</i>	—	—	—	X	X	X
<i>Otomys angoniensis</i>	—	X	—	X	X	—
<i>Otomys saundersiae</i>	—	—	X	—	X	—
<i>Otomys irroratus</i>	—	X	X	X	X	X
<i>Otomys sloggetti</i>	—	—	—	—	X	—
<i>Otomys unisulcatus</i>	—	X	—	—	—	—
<i>Desmodillus auricularis</i>	X	X	—	—	—	—
<i>Gerbillurus vullinus</i>	X	X	—	X	—	—
<i>Gerbillurus tytonis</i>	X	—	—	—	—	—
<i>Gerbillurus paeba</i>	X	X	X	X	—	—
<i>Gerbillurus setzeri</i>	X	—	—	—	—	—
<i>Tatera leucogaster</i>	X	X	—	X	—	—
<i>Tatera afra</i>	—	—	X	—	—	—
<i>Tatera brantsii</i>	—	X	—	X	X	—
<i>Tatera inclusa</i>	—	—	—	X	—	—

Table 1.—*Continued.*

Taxa	Biotic Zones					
	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
Total (275 species)	43	136	50	209	91	73
Percentage of total fauna	15.6	49.5	18.2	76.0	33.1	26.6
Total no. of endemic species	2	16	7	60	3	12
Percentage endemics to total zonal fauna	4.65	11.76	14.00	28.71	3.30	16.44

DISCUSSIONS

It must be stressed that subcontinental distributional data is as yet incomplete for the majority of species, particularly so in the Cape Province and South West Africa. Furthermore, the accuracy of this analysis will be greatly enhanced if conducted on the subspecies level, rather than on a species level. This ideal will be delayed for many years as a result of the unsatisfactory status of the knowledge of subspeciation in southern African mammals.

On the other hand, a more intimate knowledge of the distribution patterns of species does not necessarily imply a high incidence of range extensions into biotic zones where they have previously been unrecorded. When species' geographic ranges are better known and the occurrence of not too many species are recorded in new zones, the results of this analysis will not change dramatically. A more accurate FRF analysis facilitated by subspecies consideration will probably only enhance the find-

ings of this treatment because a higher degree of endemism is expected. Whatever the case, the following points are pertinent from Table 2 and warrant further comment here, especially with regard to my aim to assess the validity of biotic zones as viable biogeographical areas.

Superficially, the FRF indices of all zones under consideration are low enough to warrant their consideration as distinct zones (Table 2). Closer scrutiny is however essential.

The Namib is most closely related to the South West Arid, albeit with a FRF index as low as 0.458. The Namib's FRF indices when calculated against the other zones are, however, much lower, which confirms distinctness from these. The Namib possesses only two endemic species (Table 1), namely *G. tytonis* and *G. setzeri*. However, by far the greatest majority (41) of the Namib's total mammal fauna (43) consists of a faction of the bigger South West Arid fauna (some species also occur elsewhere).

Table 2.—*Resemblance of mammalian faunas of the six southern African Biotic Zones and Subzones. (See text for explanation; italic numerals on diagonal indicate total number of species in zone, the numerals in brackets underneath these denote the known number of endemic species).*

Biotic Zones	Southern Savanna Woodland	South West Arid	Southern Savanna Grassland	Forest	South West Cape	Namib
Southern Savanna Woodland	209 (60)	.580	.500	.404	.247	.238
South West Arid	100	136 (16)	.573	.201	.290	.458
Southern Savanna Grassland	75	65	91 (3)	.341	.411	.299
Forest	57	21	28	73 (12)	.309	.138
South West Cape	32	27	29	19	50 (7)	.237
Namib	30	41	20	8	11	43 (2)

Consequently it can be considered as merely a depauperate fauna of the latter, resulting from the inhospitable nature of the Namib. The Namib's biogeographical uniqueness thus lies not so much in its typical endemic fauna, or its faunal composition for that matter, but rather in the fauna it does not possess. The Namib is therefore considered here as a biotic zone of full rank. Detailed analysis has shown that the Namib can be further subdivided, on the basis of the sand dunes being faunistically more depauperate than the gravel plains (see Coetzee, 1969).

In spite of its tremendous floral diversity, the South Western Cape is also very depauperate in mammalian fauna. However, it must be pointed out that this is, in terms of intensive mammal surveying, the most neglected biotic zone of all. It has seven endemic taxa as far as is known—*C. zyli*, *M. leseuri*, *E. melckorum*, *E. notius*, *D. d. dorcas*, *T. afra*, and the extinct *H. leucophaeus* (see Table 1). The remainder of the faunal element is made up of mammalian species shared with other biotic zones. This zone shares 32 species with the Woodland zone, and 29 with the Grassland zone. However, as a result of the enormous differential species diversity between the Woodland and the South West Cape, the FRF analysis indicates a closer resemblance between the latter zone and the less diversified Grassland zone, with an index of 0.411. It is interesting to note that the South West Cape and the Grassland zones are unconnected.

The Forest zone is also quite distinct from the others. It is faunistically most closely related to the Southern Savanna Woodland subzone with a FRF index of 0.401. It possesses 12 endemic species (see Table 1).

The Woodland and Grassland zones and the South West Arid zone are the three areas related more closely to each other than any other combination of zones. Their individual FRF indices in relation to each other are however considered low enough to warrant their individual recognition. Because the Grassland has been considered a subzone of the Southern Savanna biotic zone, closest resemblance is expected between it and the related Woodland subzone. This is, however, not the case. Both in terms of absolute number of species in common and FRF index, the Woodland and South West Arid are faunistically most closely related (100 species in common; FRF index 0.580). This is followed by a closer resemblance between Grassland and South West Arid in terms of FRF indices (0.573), but in

terms of number of species in common, a closer resemblance between Grassland and Woodland (75 species). This inconsistency can be ascribed to the disproportionate sizes of the three zonal faunas and as compensated for by Duellman's formula, especially designed for such instances. The Southern Savanna Woodland has by far the richest mammalian fauna; 209 species, representing 76.0% of the total southern African mammalian fauna, occur here, including 60 endemics (predominantly bats). This is followed by the South West Arid, with a total diversity of 136 species, that is 49.5% of the total of 275 southern African species, with 16 endemics. The Savanna Woodland undoubtedly offers the highest variety of habitats, being ecologically more diversified both horizontally and vertically. Its rich species diversity could be related to this fact more than any other.

The temptation is great to assume that the respective faunal elements of other zones have originated by a radiation of Woodland-adapted species. Undoubtedly this is true in many instances, especially in the case of species, which do not rely on trees as an integral element in their habitat requirements. On the other hand, the high number of endemics typical of the Woodland and South West Arid areas combined (76 species) can be interpreted as a faunal element specialized towards a dependence on woodland in some manner or other. The fact that such a large portion (100 species) of the non-endemic fauna of the Woodland apparently radiated adaptively into the South West Arid is reflected by the highest FRF index of all (0.580). Mostly due to lower average annual precipitation, the latter zone has a less developed woodland flora, and consequently a less diversified mammalian fauna.

The same situation could also be demonstrated with Grassland-adapted species finding suitable habitat in adjacent Woodland Savanna (FRF index 0.500) and South West Arid (FRF index 0.573). Forest is scattered through three zones (Southern Savanna Woodland, Southern Savanna Grassland, and South West Cape), and has higher FRF indices with these than with the non-adjacent Namib and South West Arid. This trend of a relatively higher FRF index reflecting a sharing of species between adjacent zones, numerically radiating clinally from the Woodland Savanna, appears to be the rule. There is one exception, that is South West Cape being faunistically closest to the non-adjacent Grassland, with a FRF index of 0.423.

Nel (1975) found an almost linear correlation between number of species and mean annual precipitation in a latitudinal direction in southern Africa. The result is a low-to-high gradient in species densities from west to east, as mean annual rainfall increases. This is particularly the case with bats. Nel could also find no real correlation between species density and altitude. The altitudinal profile of southern Africa is relatively low, which probably explains this phenomenon. This, however, needs closer study to confirm its validity.

CONCLUSIONS

1) Six biotic zones are recognized as viable biogeographical entities, as deduced from this analysis. Where the Grassland and the Woodland have formerly been regarded as subzones of the then Southern Savanna biotic zone, terminology may hence be confusing when referring to these as biotic zones of full rank. In order to retain the Pan-African implications and perspective of the term Southern Savanna, I suggest that these two biotic zones be known as the Southern Savanna Woodland and the Southern Savanna Grassland biotic zones. This suggestion is made in the full realization that in the latter case, the definition of a savanna is stretched to the limit. Terminology for the Namib biotic zone remains unchanged, indicating its elevated zonal status.

2) Biotic zones are here regarded as the largest biogeographic units in which southern Africa could be subdivided, that is Southern Savanna Woodland, Southern Savanna Grassland, Forest, Namib, South West Arid, and South West Cape.

3) Very few species have such a wide habitat tolerance that they occur in all biotic zones. Endemism is, on the other hand, equally as unusual. In the majority of instances, species are shared between various combinations of zones, and the unique feature of the FRF analysis is to take this into account, apart from endemism. Therefore, a high FRF index indicates a high incidence of shared species and therefore closer faunal similarity.

4) The FRF analysis in fact takes three characteristics into consideration when expressing the faunal distinctness of a zone: the respective species densities of the two zones under consideration; the number of species in common; and indirectly the number of distinctive species of each zone. Based on the results of the FRF analysis, the Namib zone is deduced to be fully distinct from the South West

It would appear from the results of this analysis that a low-to-high gradient in species densities could also be demonstrated in a south to north direction. Species densities increase from 50 in the South West Cape, to 91 in the Grassland, to 136 in the South West Arid, to 209 in the Woodland. Although rainfall again undoubtedly plays some role in this trend, other causal factors such as decreasing latitude, temperature, faunal origin, and dispersion, will have to be considered in a more detailed analysis.

Arid. It is considered a bona fide biotic zone in full realization of the fact that it has a very small distinctive fauna. The Grassland is similarly considered to be a distinct biotic zone, rather than a subzone. In both these instances, one of the previous considerations for their recognition as zones of lower rank was the low degree of endemism.

5) The six biotic zones recognized here as biogeographical entities, correlate very well with what I regard as major ecological biomes in southern Africa.

6) The FRF indices of the South West Arid, the Woodland, and the Grassland, as compared with each other, are all over 0.500. There is no established value over which a zone cannot be considered statistically valid, and judgment is therefore subjective. The FRF value of these zones in question is here considered low enough to warrant their recognition as valid biotic zones. In comparison Armstrong (1972) considers Merriam's (1890) life zones, which the former author tested with Duellman's FRF analysis, as valid with indices as high as 0.847. In the present analysis, the generally lower FRF indices could also be ascribed to disproportionate faunal densities between certain zones. These differences between the sizes of zonal faunas are here regarded as valid criteria in considering the rank of a particular zone.

7) With the exception of seven species, the remainder of the 68 southern African bat species are all recorded from the Southern Savanna Woodland, among other zones. The presence of the bat fauna in the other biotic zones is dramatically less (five in the Namib; 20 in the South West Arid; six in the South West Cape; seven in the Grassland; and 18 in the Forest). The Chiroptera is the least known group of mammals in southern Africa, and although Duellman's (1965) formula partly compensates for

this shortcoming, it has an undetermined bearing on the accuracy of the above observation. The inference is, however, that as a group bats have a remarkable attachment to Woodland Savanna.

8) Biotic zones are empirically derived by consideration of major vegetation types. Although the former are proved to be significant from a faunal point of view, it does not necessarily reflect the best way to describe faunal distribution patterns, especially because individual geographic ranges of species seldom overlap entirely with any biotic zone. Biotic zones as significant biogeographical entities should rather, from a faunal point of view, be seen as illustrating the gross direct relationship of the animal to its floral environment, and to a lesser ex-

tent, to the physical environment. In the context of biotic zones, faunal interrelationships should therefore be interpreted from an ecological point of view.

9) Continued intensive mammal surveying in southern Africa is considered essential for a better understanding of both subspeciation and zoogeographical interpretation, through more detailed analysis. Especially the Chiroptera throughout the subcontinent, and the faunas of South West Arid and South West Cape biotic zones, need intensive attention in terms of surveying. It is, however, not expected that a more intimate knowledge of these aspects will dramatically change the results and implications of this analysis.

ACKNOWLEDGMENTS

This paper is introductory to a detailed zoogeographical analysis of distribution patterns of Transvaal mammals. It is aimed at establishing the credibility of biotic zones as major biogeographical entities within this Province in order to facilitate further subdivision into community-types. The research on the distribution of Transvaal mammals has been jointly sponsored by the Transvaal Museum and the South African Council for Scientific and Industrial Research, to whom I express my gratitude.

I am also grateful to Prof. J. Meester and Prof. J. A. J. Nel for critically reading the manuscript and making helpful suggestions.

An invitation by the Carnegie Museum of Natural History to attend a colloquium on the taxonomy and ecology of the small mammals of Africa, where this paper was presented, was gratefully accepted. I also thank the S.A. Department of National Education and the Transvaal Museum for travel grants to and from Pittsburgh, as well as Mrs. E. du Plooy for typing the manuscript.

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KARYOTYPIC DATA FOR AFRICAN MAMMALS, WITH A DESCRIPTION OF AN *IN VIVO* BONE MARROW TECHNIQUE

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ABSTRACT

Basic information, which should be included in any publication on the chromosomes of mammals, is given. A field-tested bone marrow-*in vivo* method of karyotyping is presented. A re-

view of the literature concerning karyotypes of African mammals was done and these karyotypic data are listed for 292 species and subspecies of African mammals.

INTRODUCTION

Karyotypes have proven to be valuable data for evolutionary and systematic studies. A summary of chromosomal data for African mammals is presented in Appendix I. For maximum value, any publication on the chromosomes of a species should contain the following information:

1. A photomicrograph of the karyotype. This is necessary if this is the first report for a species or if your karyotypic data differs from that previously published for the species.

2. Diploid Number.
3. "Nombre fundamental" or number of arms of the autosomal complement.
4. Morphology of sex chromosomes.
5. Sex of specimens examined.
6. Number of specimens examined.
7. Geographic origin of specimen examined.
8. Museum where voucher specimens are deposited (with museum numbers, if possible).
9. Minimum number of spreads examined from any specimen included.

METHODS AND TECHNIQUES

Preparation of somatic chromosomes is a simple process which can be conducted in the field. For the bone marrow-*in vivo* technique described below, live animals are required. The following technique is modified after Baker (1970).

1. Inject the live animal intraperitoneally with a 0.03% Vinblastine (Velban of Eli Lilly & Co.) or colchicine solution at 0.01 ml per gram of body weight.

2. After two hours sacrifice the animal and remove a long bone, such as the femur in rodents or the humerus in bats, without damaging the proximal end. Remove the flesh and a chip of bone from the proximal end to expose the red bone marrow cavity. Flush the shaft with 3 ml of a 1.0% sodium citrate solution. Pipette vigorously to break up any cell clumps. The sodium citrate solution will support bacterial growth and should be prepared daily under field conditions.

3. Let the resultant cell-suspension set for about 10 min.

4. Centrifuge the suspension at 1,500 RPM for 4 min.

5. Discard as much of the supernatant fluid as possible, being careful to leave the button of cells undisturbed. Add 3 ml of freshly prepared Carnoy's fixative (3 parts absolute methanol:1 part glacial acetic acid). Floating material and lipids may be removed at this stage. Disrupt the cell button with a pipette until the cell suspension is homogeneous. Allow cells to fix for about 10 min.

6. Centrifuge for 4 min and decant supernate. Resuspend cells in 1.0 ml of fixative and centrifuge as before. This step is repeated at least three times. After final washing, cells are resuspended in 1.0 ml of fixative.

7. Place two or three drops of cell suspension on a clean slide and ignite. When the fire extinguishes itself, the residue is promptly slung from the slide. Four slides from each specimen are usually made.

8. Dry slides are stained for 12 min in a 2% Giemsa stain (1 ml of Giemsa's stock solution in 50 ml

of buffer). Buffer is made by mixing 0.469 g of NaH_2PO_4 and 0.937 g of Na_2HPO_4 in 1,000 ml of distilled water. The buffered stain can be used to stain three or four sets of slides. If the buffer solution is unavailable, then staining can be by other methods such as one part Giemsa's stock solution to eight parts distilled water for 15 min. If staining with the latter solution is poor, heating the stain to near 50°C will often help. This distilled water base stain can be used to stain only one set of slides and then new stain must be mixed.

9. When a slide is removed from the stain it must be quickly rinsed with distilled water or a film of stain will cover the slide. Slide should be dry before covering with balsam or permount and a 22 by 40 mm coverslip.

Voucher specimens, with accurate collection data, should be deposited in a reputable museum. The tag on the voucher specimen should show that this specimen was karyotyped and microscope slides should be cross referenced to the voucher specimen.

TERMINOLOGY

Metacentric is a biarmed element that has arms of equal length (ratio is not greater than 1:1.1). Submetacentric is a biarmed element that has an arm ratio greater than 1:1.1 but less than 1:2. Subtelocentric is a biarmed element that has an arm ratio greater than 1:2, but a second short arm is clearly visible. Acrocentric (=telocentric for practical purposes) is an element that appears to be uniarmed when viewed with a light microscope. When cal-

culating the nombre fundamental or number of arms of the autosomal complement, each metacentric, submetacentric, or subtelocentric is given a value of 2, whereas each acrocentric is given a value of 1. The nombre fundamental (NF) of Matthey includes the arms of the sex elements and auto, whereas the "number of arms of the autosomal complement" (AA Appendix I) does not include the sex elements.

ACKNOWLEDGMENTS

We thank R. Laurie Robbins and Ginger Smith for assistance in preparation and editing. We thank Duane A. Schlitter and Hugh H. Genoways for organizing this symposium on African

small mammals. Without their encouragement, this manuscript would never have been produced. Supported in part by the Institute of Museum Research.

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Appendix I.—Chromosomal data for African mammals. Orders are listed in classical phylogenetic arrangement. Families, genera, and species are in alphabetical order. 2N = diploid number; NF = Nombre Fundamental, which includes sex elements; AA = number of arms of autosomal complements; BA = number of banded autosomes. M, SM, ST, and A are defined in text.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Insectivora								
Erinaceidae								
<i>Erinaceus algirus</i>	48	—	—	—	—	—	—	Gropp and Natarajan, 1972
Hemiechinus auritus								
<i>Hemiechinus auritus aegyptius</i>	48	—	—	—	X:M Y:small A	—	—	Gropp et al., 1969b
Macroscelidae								
<i>Elephantulus rufescens</i>	34	—	—	—	—	—	—	Chu and Bender, 1962
<i>Elephantulus rupestris jamesoni</i>	30	—	—	—	—	—	—	Ford and Hamerton, 1956
<i>Elephantulus rozeti</i>	28	—	—	—	—	—	—	Matthey, 1954a
<i>Nasilio b. brachyrhynchus</i>	26	—	—	—	—	—	—	Stimson and Goodman, 1966
Soricidae								
<i>Crociodura bottegii eburnea</i>	40	—	—	—	—	—	Ivory Coast	Meylan, 1971
<i>Crociodura jouvenetae ebriensis</i>	44	—	—	—	—	—	Ivory Coast	Meylan, 1971
<i>Crociodura occidentalis kiwu</i>	50	—	—	—	X:large ST Y:small A	—	—	Meylan, 1967
<i>Crociodura olivieri</i>	50	—	56	8	X:SM Y:small A	4	Egypt	de Hondt, 1974
<i>Crociodura poensis panela</i>	52	—	—	—	—	—	Ivory Coast	Meylan, 1971
<i>Crociodura russula pulchra</i>	42	—	—	—	—	—	Ivory Coast	Meylan, 1971
<i>Crociodura suaveolens</i>	40	—	—	—	—	—	—	Meylan, 1966
<i>Crociodura theresae</i>	50	—	—	—	—	—	Ivory Coast	Meylan, 1971
<i>Sylviores megalura</i>	48	96	—	46	—	1♂	Ivory Coast	Meylan, 1975
Tenrecidae								
<i>Micropotamogale lanottei</i>	38	76	—	—	—	—	Ivory Coast	Vogel et al., 1977
Chiroptera								
Molossidae								
<i>Otomops martiensseni</i>	48	—	56	—	X:SM; Y:A	1	—	Dulić and Mutere, 1973
<i>Platymops setiger</i>	48	—	54	—	X&Y:SM	1	—	Warner et al., 1974
<i>Tadarida bivitata</i>	48	—	54	8	X:M; Y:A	4	Kenya, Rhodesia	Peterson and Nagorsen, 1975
<i>Tadarida condylura</i>	48	—	56	—	X:SM; Y:A	6	—	Dulić and Mutere, 1973

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Tadarida fulminans</i>	48	—	54	8	X:SM; Y:A	4	Rhodesia	Peterson and Nagorsen, 1975
<i>Tadarida pumila</i>	48	—	58	—	X:SM; Y:SM	9	—	Dulić and Mutere, 1973
Nycteridae								
<i>Nycteris thebaica</i>	42	—	78	38	X:SM; Y:small M	6	Rhodesia	Peterson and Nagorsen, 1975
Pteropidae								
<i>Eidolon helvum</i>	34	—	—	—	—	—	—	Matthey, 1962
<i>Epomophorus anurus</i>	36	72	—	—	—	1 ♀	—	Dulić and Mutere, 1973b
<i>Epomophorus crypturus</i>	35 (♂)	—	68	34	—	1 ♂, 1 ♀	Rhodesia	Peterson and Nagorsen, 1975
<i>Epomophorus gambianus</i>	36 (♀)	—	68	34	X:SM	2 ♀ ♀	Rhodesia	Peterson and Nagorsen, 1975
<i>Epomophorus wahlbergi</i>	36	72	—	—	X:SM; Y:A	1 ♂	—	Dulić and Mutere, 1973b
	36	—	68	34	—	2 ♀ ♀	Rhodesia	Dulić and Mutere, 1977
<i>Epomops franqueti</i>	36	—	68	34	—	2 ♀ ♀	Kenya	Peterson and Nagorsen, 1975
<i>Rousettus aegyptiacus</i>	36	—	66	—	X:SM; Y:minute	—	—	Peterson and Nagorsen, 1975
<i>leachi</i>								Dulić and Mutere, 1973b
Rhinolophidae								
<i>Aselia tridens</i>	50	—	62	14	X:ST; Y:A	9	Tunisia	Baker et al., 1975
<i>Hipposideros caffer</i>	32	—	60	30	X:ST; Y:A	2	Rhodesia	Peterson and Nagorsen, 1975
	32	—	60	30	X:M	1	Kenya	Dulić and Mutere, 1973b
<i>Rhinolophus clivus</i>	58	—	62	6	X:large A; Y:small A	4	—	Dulić and Mutere, 1974
<i>Rhinolophus darlingi</i>	50	—	60	4	X&Y:ST	2	Rhodesia	Peterson and Nagorsen, 1975
<i>Rhinolophus denti</i>	58	—	62	6	X:ST	2	Rhodesia	Peterson and Nagorsen, 1975
<i>Rhinolophus euryale</i>	58	—	60	—	—	—	Europe	Bovey, 1949
								Manfredi Romanini et al., 1975
<i>Rhinolophus ferrumequinum</i>	58	—	60	4	X:SM; Y:A	2 ♂ ♂	Tunisia	Baker et al., 1975

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Galago demidovii</i>	58	—	—	—	—	—	—	de Boer, 1972b
<i>Galago senegalensis</i>	36–38	variable	—	—	X:SM; Y:SM or A	—	—	Matthey, 1955 Egozcue, 1970 Chu and Bender, 1961 Chiarelli, 1974
<i>Perodicticus potto</i>	62	87	—	—	X:SM; Y:A	—	—	Chiarelli, 1966
Cercopithecidae								
<i>Allenopithecus nigroviridis</i>	60	—	—	—	—	—	—	Hsu and Benirschke, 6(299), 1971 Chiarelli, 1962 Chu and Bender, 1961 Chu and Giles, 1957 Hsu and Benirschke, 5(246), 1971
<i>Cercocebus aterrimus</i>	42	—	—	—	—	—	—	Chu and Giles, 1957
<i>Cercocebus galeritus</i>	42	—	—	—	—	—	—	Hsu and Benirschke, 5(246), 1971
<i>Cercocebus torquatus</i>	42	—	80	40	X:SM; Y:M	—	—	Chu and Giles, 1957
<i>Cercopithecus aethiops sabaeus</i>	60	—	116	58	X:large SM; Y:small SM	—	—	Chu and Giles, 1957 Hsu and Benirschke, 1(48), 1967 Wurster and Benirschke, 1969
<i>Cercopithecus ascanius</i>	66	—	112	48	X:SM; Y:small A	—	—	Hsu and Benirschke, 6(300), 1971 Chiarelli, 1963 Hsu and Benirschke, 5(247), 1971 Chu and Giles, 1957 Chiarelli, 1962b
<i>Cercopithecus cephus</i>	66	—	108	44	X&Y:SM	—	—	de Boer, 1970 Chu and Bender, 1961 Bender and Chu, 1963 Chu and Giles, 1957
<i>Cercopithecus diana</i>	60	—	—	—	—	—	—	Tappen, 1960
<i>Cercopithecus diana roloway</i>	58	—	—	—	—	—	—	Bender and Mettler, 1958
<i>Cercopithecus hamlyni</i>	64	—	—	—	—	—	—	Chiarelli, 1962
<i>Cercopithecus lhoesti</i>	72	—	—	—	—	—	—	Kuhn, 1967
<i>Cercopithecus mitis</i>	72	—	—	—	—	—	—	
<i>Cercopithecus mona campbelli</i>	66	—	—	—	—	—	—	
<i>Cercopithecus mona denti</i>	66	—	—	—	—	—	—	
<i>Cercopithecus mona mona</i>	66	—	—	—	—	—	—	
<i>Cercopithecus mona preussi</i>	66	—	—	—	—	—	—	
<i>Cercopithecus nictians</i>	70	—	—	—	—	—	—	

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Cercopithecus</i>								
<i>petaurista</i>	66	—	—	—	—	—	—	Chu and Giles, 1957
<i>butikoferi</i>	44	—	—	—	—	—	—	Kuhn, 1967
<i>Colobus badius</i>	44	—	—	—	—	—	—	Chiarelli, 1962
<i>Calobus polycomos</i>	54	—	—	—	—	—	—	Chu and Giles, 1957
<i>Erythrocebus patas</i>	54	—	86	38	X:SM; Y:small SM	—	—	Chiarelli, 1962
<i>Miopithecus talapoin</i>								Hsu and Benirschke, 5(248), 1971
<i>Papio</i> sp. (<i>anubis</i> ?)	42	—	80	40	X:SM; Y:small A	—	—	Darlington and Hague, 1955
								Hsu and Benirschke, 5(248), 1971
<i>Papio cynocephalus</i>	42	—	—	—	—	—	—	Chiarelli, 1962
<i>Papio gelada</i>	42	—	—	—	—	—	—	Chiarelli, 1962
<i>Papio hamadryas</i>	42	—	—	—	—	—	—	Chiarelli, 1962
<i>Papio leucophaeus</i>	42	—	—	—	—	—	—	Chiarelli, 1962
<i>Papio papio</i>	42	—	—	—	—	—	—	Darlington and Hague, 1955
<i>Papio ursinus</i>	42	—	—	—	—	—	—	Ismail and Tobias, 1956
Pongidae								
<i>Gorilla gorilla</i>	48	—	78	32	X:large SM, Y:small SM	—	—	Hamerton et al., 1961
								Hsu and Benirschke, 5(150), 1969
								Hamerton et al., 1963
<i>Gorilla gorilla beringei</i>	48	—	80	34	X:SM; Y:small A	—	—	Young et al., 1960
<i>Pan troglodytes</i>								Chiarelli, 1962
<i>Pan troglodytes paniscus</i>	48	—	—	—	—	—	—	Hsu and Benirschke, 3(148), 1969
								Chiarelli, 1961
Lagomorpha								
Leporidae								
<i>Lepus capensis tolai</i>	48	—	—	—	—	—	—	Vorontsov and Ivanitskaia, 1969
<i>Oryctolagus cuniculus</i>	44	72	—	—	X:SM; Y:SM	—	—	Melander, 1956
								Hsu and Benirschke, 1(8), 1967

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
Rodentia								
Bathyrigidae								
<i>Georchus capensis</i>	54	—	—	—	—	—	—	Matthey, 1956
Muridae								
Cricetinae								
<i>Mysromys</i>	32	—	—	—	—	—	South Africa	Matthey, 1954c
<i>albicaudatus</i>	32	—	60	30	X&Y:A	—	—	Hsu and Benirschke, 2(60), 1958
Dendromurinae								
<i>Dendromus insignis</i>	48	—	—	—	—	—	—	Matthey, 1967
<i>kiivu</i>	36	—	—	—	—	—	—	Matthey, 1970
<i>Dendromus melanotis</i>	38	—	—	—	—	—	—	Matthey, 1970
<i>Dendromus mystacalis</i>	38	—	—	—	—	—	—	—
<i>messorius</i>	38	—	—	—	—	—	—	Allenbach, 1964
<i>Malacothrix typica</i>	46	—	—	—	X:SM	—	South Africa	Matthey, 1958
<i>Saccostomus</i>	44	—	—	—	—	—	—	Ford and Hamerton, 1956
<i>campestris</i>	40–42	—	—	—	—	4	Ethiopia	Hubert, 1978a
<i>Saccostomus mearnsi</i>	68	70	—	—	X:M; Y:SM	—	South Africa	Matthey, 1954c
<i>Statomys pratensis</i>	52	70	—	—	X&Y:M	—	South Africa	Matthey, 1954c
Gerbillinae								
<i>Desmodillus aricularis</i>	36	—	—	—	—	—	—	Matthey, 1958
<i>Gerbillurus pacha</i>	40	80	—	—	—	—	—	Wahrman and Zahavi, 1955
<i>Gerbillus allenbyi</i>	52	61, 62	—	—	—	—	Egypt	Wassiff et al., 1969
<i>Gerbillus aeneus</i>	40	80	—	38	—	—	Egypt	Wassiff et al., 1969
<i>Gerbillus andersoni</i>	40	—	76	—	—	—	Tunisia	Cockrum et al., 1977
<i>Gerbillus aureus</i>	74	—	92–100	20–28	X:SM; Y:A?	—	Tunisia	Jordan et al., 1975
<i>Gerbillus calurus</i>	38	74	—	—	—	—	Egypt	Wahrman and Zahavi, 1955
(= <i>Sekeetamys calurus</i>)	56	—	—	—	—	—	—	Wassiff et al., 1969
<i>Gerbillus campestris</i>	56	69–71	—	—	—	—	Egypt	Matthey, 1953
	56	—	68	7	X&Y:SM	—	Tunisia	Wassiff et al., 1969
<i>Gerbillus dasyurus</i>	60	66–68	—	—	—	—	Israel and N. Africa	Jordan et al., 1975
	60	69–70	—	—	—	—	Egypt	Wahrman and Zahavi, 1955
<i>Gerbillus garamantis</i>	54	—	—	—	—	—	—	Wassiff et al., 1969
<i>Gerbillus gerbillus</i>	43 (♂)	79–81	—	—	—	—	—	Matthey, 1954c
	42 (♀)	—	—	—	—	—	—	Matthey, 1954d
	43 (♂)	—	74	18	X:ST; YY (♂):M?	—	Egypt	Wassiff et al., 1969
	42 (♀)	—	—	—	—	—	Tunisia	Jordan et al., 1975

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Gerbillus henleyi</i>	52	63-65	—	—	—	—	Egypt	Wassiff et al., 1969
<i>Gerbillus nanus</i>	52	66-68	—	—	—	—	—	Wahman and Zahavi, 1955
	52	—	—	—	—	—	Egypt	Wassiff et al., 1969
	52	—	58	4	X:M; Y:A	9	Tunisia	Jordan et al., 1975
<i>Gerbillus nigeriae</i>	62-68	92-102	—	—	X:large A	—	Niger	Tranier, 1976a
<i>Gerbillus perpallidus</i>	40	—	—	—	—	—	—	Lay, 1975
<i>Gerbillus pulvinatus</i>	62	84	—	—	—	14	Ethiopia	Hubert, 1978b
<i>Gerbillus pyramidum</i>	40	80	74	18	—	—	Algeria	Matthey, 1952
	38	76	72	—	—	—	Egypt	Wassiff et al., 1969
	40	—	—	—	X&Y:M	—	Tunisia	Jordan et al., 1975
	40	78	—	—	—	1	Senegal	Hubert and Bohme, 1978
<i>Gerbillus simoni</i> (kaiserii)	60	68-69	—	—	—	—	Egypt	Wassiff et al., 1969
<i>Gerbillus tarabuli</i>	60	—	—	8-10	—	—	Tunisia	Cockrum et al., 1976
<i>Meriones crassus</i>	40	—	—	—	—	—	—	Lay, 1975
	60	60	—	—	—	—	—	Matthey, 1953
	60	74	—	—	—	—	—	Nadler and Lay, 1967
<i>Meriones libycus</i>	44	80-82	—	—	—	—	—	Matthey, 1953
	44	74	—	—	—	—	—	Nadler and Lay, 1967
	44	—	72	30	X:A; Y:SM	—	—	Hsu and Benirschke, 5(226), 1971
<i>Meriones shawi</i>	44	74	—	—	—	—	—	Matthey, 1957
	44	—	72	30	X&Y:SM	—	—	Hsu and Benirschke, 5(227), 1971
<i>Pachyuromys duprasi</i>	54	—	—	—	—	—	—	Matthey, 1954e
<i>Psammomys obesus</i>	48	—	—	—	—	—	—	Matthey, 1954e
	48	—	74	28	X:large SM; Y:small M	—	—	Hsu and Benirschke, 4(170), 1970
<i>Tatera afra</i>	44	70-76	—	—	—	—	South Africa	Matthey, 1954c
<i>Tatera brantsi draco</i>	44	70-76	—	—	X&Y:M	—	South Africa	Matthey, 1954c
<i>Tatera gambiana</i>	52	—	—	—	—	—	Senegal	Hubert et al., 1973
<i>Tatera guineae</i>	50	—	—	—	—	—	—	Matthey and Petter, 1970
<i>Tatera hopkinsoni</i>	48	—	—	—	—	—	Upper Volia	Matthey and Petter, 1970
<i>Tatera kempi</i>	36	—	—	—	—	—	C.A.E.	Matthey and Petter, 1970
<i>Tatera nigrita</i>	48	66, 70	—	—	—	—	Chad	Tranier, 1974
<i>Tatera robusta</i>	46	—	—	—	—	—	—	Matthey and Petter, 1970
<i>Tatera schinzi</i>	42	70-76	—	—	X&Y:M	—	—	Matthey, 1954c
<i>Tatera valida</i>	52	—	—	—	—	—	—	Matthey, 1969
<i>Taterillus arenarius</i> *	30	—	36	—	X:large M; Y:?	1 ♀	Mauritania	Robbins, 1974

*(specimen =
T. nigeriae of
Matthey, 1969)

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
<i>Taterillus congicus</i>	54	68	—	—	—	—	C.A.E.	Matthey and Petter, 1970
	54	70	66	14	—	—	Chad	Tranier et al., 1974
	54	—	64	—	X:large SM; Y:small SM	—	C.A.E.	Genest and Petter, 1970
<i>Taterillus gracilis</i>	23 (♂)	—	—	—	—	—	Senegal	Robbins, 1977
	22 (♀)	—	—	—	—	—	—	Matthey, 1969
	37 (♂)	46, 48	—	—	X:M; Y:SM	—	Upper Volta	Matthey and Jotterand, 1972
	36 (♀)	—	—	—	—	—	Senegal	Robbins, in press
	37 (♂)	—	44	—	—	—	—	Matthey and Petter, 1970
	36 (♀)	—	—	—	—	—	Upper Volta	Robbins, in press
	37 (♂)	—	42	—	—	—	Ghana	Matthey and Petter, 1970
	36 (♀)	—	—	—	—	—	Ivory Coast	Robbins, in press
<i>Taterillus harringtoni</i> * * (following specimens reported as <i>T. emini</i>)	44	—	—	—	—	1	Somalia	Matthey, 1969
	44	—	—	—	—	1	Ethiopia	Genest and Petter, 1973
	44	—	62	—	X:large SM; Y:medium SM	—	C.A.E. Kenya	Robbins, 1973
<i>Taterillus lacustris</i>	28	48	—	18	X:large M; Y:small M	2	Cameroon	Tranier et al., 1974
<i>Taterillus nigeriae</i>	30	—	—	—	—	—	—	Matthey, 1969
<i>Taterillus</i> sp.	18 (♀)	32–34	26, 28	10, 12	X:large SM; Y:small M	4	Niger	Tranier, 1974b
	19 (♂)	—	—	—	—	—	—	Matthey, 1969
<i>Taterillus pygargus</i>	22–23	40–44	—	—	X:large SM; Y:small M; Y ₂ :medium SM	—	Senegal	Matthey, 1969
	23 (♂)	40–44	—	—	—	—	—	Petter et al., 1972
	22 (♀)	—	—	—	—	—	—	Matthey and Jotterand, 1972
Murinae								
<i>Acomys aircensis</i> (<i>cahirinus</i>)	42	70	—	28	—	—	Niger	Tranier, 1976b
<i>Acomys subspinosus</i>	64	72	—	6	X:large SM	—	South Africa	Matthey, 1965
<i>Aethomys bocagei</i>	50	—	—	—	—	—	—	Matthey, 1963a
<i>Aethomys chrysophilus</i>	44	—	—	—	—	—	—	Matthey, 1958
<i>Aethomys granti</i>	32	—	—	—	—	—	—	Matthey, 1964
<i>Aethomys namaquensis</i>	24	—	—	—	—	—	—	Matthey, 1964
<i>Apodemus sylvaticus</i>	48	—	—	—	—	—	—	Matthey, 1936
	48	—	46	0	X&Y:A	—	Europe	Hsu and Benirschke, 4(176), 1970

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Arvicanthus</i>	62	—	—	—	—	—	—	Matthey, 1959
<i>abyssinicus</i>								
<i>Arvicanthus niloticus</i>	56	—	—	—	—	—	C.A.E.	Matthey, 1965
<i>Cricetomys gambianus</i>	78	—	—	—	X:SM	—	—	Matthey, 1953 ^c
<i>Dasymys incomptus</i>	38	—	—	4	X&Y:A	—	Ivory Coast	Matthey, 1958
<i>rufulus</i>								
<i>Hybomys univittatus</i>	48	—	—	—	—	—	—	Matthey, 1959
<i>Hylomyscus aeta</i>	52	—	—	—	—	—	—	Matthey, 1963 ^a
	52	—	—	—	—	2	Fernando Po	Eisentraut, 1969
<i>Hylomyscus alleni</i>	46	—	—	—	—	3	Fernando Po, Cameroon	Eisentraut, 1969
<i>Hylomyscus stella</i>	46	—	—	—	—	—	—	Matthey, 1963 ^a
	46	—	—	—	—	4	Fernando Po, Cameroon	Eisentraut, 1969
<i>Lemniscomys barbarus</i>	54	60	—	—	X&Y:M	—	—	Matthey, 1954 ^c
<i>Lamniscomys bellieri</i>	56	78	74	10	X:M; Y:M	8	Ivory Coast	Van der Straeten and Verheyen, 1978
<i>Lemniscomys striatus</i>	48	—	—	—	—	—	—	Matthey, 1959
	44	72	68	26	X:M; Y:small M?	15	Ivory Coast	Van der Straeten and Verheyen, 1978
								Matthey, 1967 ^a
<i>Lophuromys aquilus</i>	70	—	—	—	—	—	—	Dieterlen, 1976
<i>laticeps</i>								
<i>Lophuromys</i>	70	—	—	—	—	—	—	
<i>flavopunctatus</i>								
<i>Lophuromys s.</i>	60	—	—	—	X:SM; Y:M	—	Ivory Coast	Matthey, 1958
<i>sikapusi</i>								
<i>Lophuromys woosnomi</i>	42	—	—	—	—	—	—	Dieterlen, 1976
<i>Malacomys edwardsi</i>	48	48	—	0	X&Y:A	—	Ivory Coast	Matthey, 1958
<i>Mastomys erythroleucus</i>	40	—	—	—	X:M; Y:SM	—	Ivory Coast	Matthey, 1958
	38	48-52	—	—	—	—	—	Matthey, 1966 ^a , 1965
	38	54	—	—	—	—	Senegal, Morocco	Tranier, 1975
							Zaire	
<i>Mastomys natalensis</i>	38	—	—	—	—	—	—	Matthey, 1967 ^a
(= <i>M. coucha</i>)	36	—	—	—	X&Y:SM	—	South Africa	Matthey, 1954 ^c
								Petter and Genest, 1970
	36	—	44	10	X:large SM; Y:ST	—	—	Hsu and Benirschke, 2(71), 1968
<i>Mastomys cf. huberti</i>	36	—	—	—	—	—	Rhodesia	Lyons et al., 1977
	32	—	—	—	—	—	Zaire	Matthey, 1966 ^d
							Senegal	Hubert et al., 1973
	32	52	—	—	—	—	Chad	Matthey, 1955
							C.A.E.	Matthey, 1963 ^a
<i>Mus (Leggada) bellus</i>	30	32	—	—	X:M; Y:A	—	—	Jottrand, 1972
<i>Mus (Leggada) bufo</i>	36	36	—	—	X:SM; Y:A	—	—	Matthey, 1967 ^c Jottrand, 1972

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
<i>Mus (Leggada) goundae</i>	16–19	30	—	—	X&Y:M	6	C.A.E.	Jotterand, 1972
<i>Mus (Leggada) haussa</i>	32–34	38	—	—	—	—	Ivory Coast	Matthey, 1967b Jotterand, 1972
<i>Mus (Leggada) indutus (deserti)</i>	36	36	—	—	—	—	South Africa	Matthey, 1964b Jotterand, 1972
<i>Mus (Leggada) mattheyi</i>	36	36	—	—	—	—	Ivory Coast	Matthey, 1966c Jotterand, 1972
<i>Mus (Leggada) minutoides</i>	32	36	—	—	X:M; Y:SM	—	Senegal	Petter et al., 1971
<i>Mus (Leggada) minutoides/</i>	18–34	36	—	—	variable	—	Ivory Coast	Matthey, 1958
<i>musculoides</i>	28	30–34	—	—	X:M, Y:A	50	—	Jotterand, 1972
<i>Mus (Leggada) oubanguii</i>	36	36	—	—	—	—	Ivory Coast	Matthey, 1964b Jotterand, 1972
<i>Mus (Leggada) setulosus</i>	32	34	—	—	—	—	Zaire	Matthey, 1966b
<i>Mus (Leggada) triton</i>	20–22	34 (♂) 32 (♀)	—	—	—	—	Tanzania	Matthey, 1963b
<i>Myiomys dybowskyi</i>	42	—	—	—	X:SM; Y:A	—	—	Jotterand, 1972
<i>Myiomys daltoni</i>	36	—	—	—	—	—	—	Matthey, 1970
<i>Oenomys hypoxanthus</i>	32	—	—	—	—	—	—	Matthey, 1964
<i>Pelomys campaneae</i>	48	—	—	—	—	—	—	Matthey, 1963
<i>Pelomys hartwigi</i>	34	—	—	—	—	—	—	Matthey, 1963
<i>Praomys jacksoni</i>	28	—	—	—	—	—	Cameroon	Eisentraut, 1968
<i>Praomys lukolelae</i>	28	—	—	—	—	—	—	Matthey, 1958
<i>Praomys morio</i>	42	—	—	—	—	—	C.A.E.	Petter, 1964
<i>Praomys taitae</i>	42	—	—	—	—	—	C.A.E.	Matthey, 1970
<i>Praomys tullbergi</i>	48	—	—	—	—	—	C.A.E.	Matthey, 1965
<i>Praomys tullbergi tullbergi</i>	34	34	—	0	X&Y:A	—	—	Matthey, 1965
<i>Praomys t. minor</i>	34	—	—	—	—	—	Ivory Coast	Matthey, 1958
<i>Praomys verreauxi</i>	42	—	—	—	—	—	C.A.E.	Petter, 1975
<i>Rhabdomys pumilio</i>	48	56	—	8	—	—	—	Matthey, 1965
<i>Thallomys paedulus</i>	48	—	—	—	—	—	South Africa	Matthey, 1954c Matthey, 1959
<i>Thallomys surdaster</i>	52	66	62	12	X&Y:SM	—	—	Matthey, 1971
<i>Thannomys buntingi</i>	52	66	—	12	X&Y:SM	3	Ivory Coast	Petter and Tranter, 1975
<i>Thannomys gazellae</i>	52	66	—	12	X&Y:SM	6	Ivory Coast	Petter and Tranter, 1975
	68–76	—	—	—	X:M	5	C.A.E.	Petter and Tranter, 1976

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Felis margarita</i>	38	—	—	—	—	—	—	Jotterand, 1971
<i>Felis nigripes</i>	38	—	70	—	—	—	—	Hsu and Arrighi, 1966
	38	—	68	32	X:M; Y:small M	—	—	Hsu and Benirschke, 2(83), 1968
<i>Felis serval</i>	38	—	68	32	X:M; Y:small SM	—	—	Wurster and Benirschke, 1968
<i>Panthera pardus</i>	38	—	68	32	X:medium SM; Y:small ST	—	—	Hsu and Benirschke, 5(235), 1971
								Hsu, 1960
								Hsu and Benirschke, 2(84), 1968
Hyaenidae								
<i>Crocuta crocuta</i>	40	—	58	20	X:M; Y:SM	—	—	Wurster and Gray, 1967
								Hsu and Benirschke, 2(78), 1968
<i>Hyaena brunnea</i>	—	—	—	—	—	—	South Africa	Wallace and Fairall, 1970
<i>Hyaena hyaena</i>	40	—	70	—	X:SM; Y:A	—	—	Wurster, 1973
<i>Proteles cristatus</i>	40	—	—	—	—	—	—	Hsu and Arrighi, 1966
	40	—	68	30	X:M; Y:small M	—	—	Ulbrich and Schmitt, 1968
								Hsu and Benirschke, 3(123), 1969
Viverridae								
<i>Atilax pallidinosus</i>	35 (♂) 36 (♀)	—	68	28	X:M; Y:?	—	—	Todd and Pressman, 1967
								Hsu and Benirschke, 3(124), 1969
<i>Bdeogale sp.</i>	36	—	68	28	X&Y:SM	—	—	Wurster and Benirschke, 1967a
								Hsu and Benirschke, 5(232), 1971
<i>Bdeogale nigripes</i>	36	—	—	—	—	—	—	Fredga, 1972
<i>Civettictis civetta</i>	38	—	—	—	—	—	—	Todd, 1967
<i>Crossarchus obscurus</i>	36 (♂)	—	—	—	—	—	—	Fredga, 1972
<i>Cynictis penicillata</i>	36	—	—	—	—	—	—	Fredga, 1972
<i>Genetta genetta</i>	54	—	—	—	—	—	—	Matthey, 1965b
<i>Genetta genetta neumanni</i>	52	—	92	46	X:SM; Y:A	—	—	Wurster and Benirschke, 1968
								Hsu and Benirschke, 3(126), 1969

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Helogale parvula</i>	36	—	—	—	—	—	—	Fredga, 1972
<i>Herpestes ichneumon</i>	48	—	—	—	—	—	—	Wurster and Benirschke, 1968
<i>Herpestes pulverulentus</i>	39 (♂)	—	—	—	—	—	—	Fredga, 1972
<i>Herpestes sanguineus</i>	40 (♀)	—	—	—	—	—	—	Fredga, 1972
	41 (♂)	—	—	—	—	—	—	Fredga, 1972
	42 (♀)	—	—	—	—	—	—	Fredga, 1972
<i>Ichneumia albicauda</i>	36	—	—	—	—	—	—	Wurster and Benirschke, 1967 ^a
<i>Mungos mungo</i>	36	—	—	—	—	—	—	Wurster and Benirschke, 1967 ^a
<i>Nandinia binotata</i>	38	—	—	—	—	—	—	Todd, 1967
<i>Suricata suricatta</i>	36	—	68	34	X:SM; Y:T	—	—	Todd, 1966
								Hsu and Benirschke, 1(30), 1967
Tubulidentata								
Orycteropidae								
<i>Orycteropus afer</i>	20	—	36	18	X:SM; Y:SM	—	—	Benirschke et al., 1970
								Hsu and Benirschke, 5(238), 1971
Proboscidea								
Elephantidae								
<i>Loxodonta africana</i>	56	—	58	4	X:SM; Y:A	—	—	Hungerford et al., 1966
								Hsu and Benirschke, 6(288), 1971
Hyracoidea								
Procaviidae								
<i>Procavia capensis</i>	54	—	62	10	X:SM; Y:small SM	—	—	Hungerford and Snyder 1969
								Hsu and Benirschke, 6(289), 1971
Perissodactyla								
Equidae								
<i>Equus asinus</i>	62	—	98	38	X:SM; Y:A	—	—	Benirschke et al., 1962
								Hsu and Benirschke, 1(33), 1967
	62	—	—	—	—	—	—	Benirschke and Malouf, 1965

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Equus burchelli antiquorum</i>	44	—	78	36	X:SM; Y:M	2	—	Benirschke and Malouf, 1965
<i>Equus burchelli bohni</i>	44	—	—	—	—	—	—	Benirschke et al., 1963
<i>Equus burchelli burchelli</i>	44	—	—	—	X:M; Y:small M	5	South Africa	Heinichen, 1970
<i>Equus burchelli crawshayi</i>	44	—	—	—	—	—	—	Benirschke et al., 1963
<i>Equus grevyi</i>	44	—	—	—	X:M; Y:small M	4	South W. Africa	Heinichen, 1970
	44	—	—	—	X:M; Y:small M	5	Rhodesia	Heinichen, 1970
	46	—	76	32	X:M; Y:small M	—	—	Mutton et al., 1964
<i>Equus quagga</i>	44	—	76	34	X:M; Y:small A?	—	—	Hsu and Benirschke, 5(240), 1971
								Benirschke and McFeeley, 1963
								Hsu and Benirschke, 5(240), 1971
<i>Equus zebra hartmannae</i>	32	—	56	26	X:SM; Y:minute	2	—	Benirschke and Malouf, 1965
	32	—	56	24	X:SM; Y:minute	—	—	Benirschke, 1967
								Hsu and Benirschke, 1(37), 1967
<i>Equus zebra zebra</i>	32	—	—	—	—	6	South Africa	Heinichen, 1970
	32	—	—	—	X:large SM; Y:small SM	4	South Africa	Heinichen, 1970
Rhinocerotidae								
<i>Ceratotherium s. sinum</i>	84	—	—	—	X:M; Y:A	11	South Africa	Heinichen, 1970
<i>Diceros bicornis</i>	84	—	—	—	—	—	—	Hungerford et al., 1967
	84	—	—	—	X:M	2	South Africa	Heinichen, 1970
Artiodactyla								
Bovidae								
<i>Addax nasomaculatus</i>	58	—	—	—	—	—	—	Wurster and Benirschke, 1968b
<i>Aepyceros melampus</i>	58-60	—	—	—	—	—	—	Wallace and Fairall, 1967a
	60	—	58	0	X:A; Y:M	—	—	Wurster and Benirschke, 1967b
								Hsu and Benirschke, 4(188), 1970

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
<i>Alcelaphus boselaphus</i>	40	—	—	—	—	—	—	Wurster and Benirschke, 1967b
<i>Anidorcas marsupialis</i>	56	—	58	4	X:A; Y:small M	—	—	Wurster and Benirschke, 1967b Hsu and Benirschke, 2(89), 1968 Robinson and Skinner, 1976 Wurster and Benirschke, 1967b
<i>Ammotragus lervia</i>	58	—	58	2	X:A; Y:small M	—	—	Wurster and Benirschke, 1967b Hsu and Benirschke, 3(137), 1969 Hauschleek-Jungen and Meili, 1967 Hsu and Benirschke, 3(140), 1969 Hard, 1969 Koulischer et al., 1967 Hard, 1969 Hard, 1969 Hard, 1969 Hard, 1969 Hard, 1969 Hsu and Benirschke, 5(242), 1971 Wurster and Benirschke, 1968b Hsu and Benirschke, 6(292), 1971 Wurster and Benirschke, 1968b Wurster and Benirschke, 1967b Hsu and Benirschke, 6(293), 1971 Wurster and Benirschke, 1968b Wurster, 1972 Wurster, 1972
<i>Capra ibex</i>	60	—	58	0	X:A; Y:small M	—	—	
<i>Cephalophus dorsalis</i>	60	—	—	—	—	—	—	
<i>Cephalophus grimmii</i>	60	—	—	—	—	—	—	
<i>Cephalophus jentinki</i>	60	—	—	—	—	—	—	
<i>Cephalophus maxwelli</i>	60	—	—	—	—	—	—	
<i>Cephalophus niger</i>	60	—	—	—	—	—	—	
<i>Cephalophus rufilatus</i>	60	—	—	—	—	—	—	
<i>Cephalophus sylvicultor</i>	60	—	58	0	X:SM; Y:A	—	—	
<i>Connochaetes gnou</i>	58	—	58	2	X&Y:A	—	—	
<i>Connochaetes taurinus</i>	58	—	—	—	—	—	—	
<i>Damaliscus dorcas</i>	38	—	58	22	X&Y:A	—	—	
<i>Gazella dama</i>	38	—	—	—	—	—	—	
<i>Gazella dorcas</i>	31 (♂) 32 (♀) 35 (♂) 32 (♀)	—	—	—	—	—	—	
<i>Gazella gazella</i>		—	—	—	—	—	—	

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
<i>Gazella thomsoni</i>	58	—	60	4	X:medium SM; Y:small M	—	—	Nelson-Rees et al., 1967 Hsu and Benirschke, 2(93), 1968
<i>Hippotragus niger</i>	60	—	58	0	X:large ST; Y:small A	—	—	Wurster and Benirschke, 1968b Hsu and Benirschke, 3(142), 1969
<i>Kobus ellipsiprymnus</i>	50	—	—	—	—	—	—	Wurster and Benirschke, 1968b
<i>Kobus kob</i>	50	—	58	10	X:A; Y:M	—	—	Taylor et al., 1967 Hsu and Benirschke, 3(143), 1969
<i>Kobus megaceros</i>	52	—	—	—	—	—	—	Wurster and Benirschke, 1968b
<i>Oryx gazella</i>	56	—	58	4	X&Y:A	—	—	Hsu and Benirschke, 2(94), 1968
<i>Oryx tao</i>	58 (♀)	—	—	—	—	—	—	Wurster, 1972
<i>Raphicerus campestris</i>	—	—	—	—	—	—	—	Wallace and Fairall, 1967c
<i>Syncerus caffer caffer</i>	52	—	58	8	X:large A; Y:small A	—	—	Ulrich and Fischer, 1967 Hsu and Benirschke, 3(145), 1969
<i>Syncerus caffer nanus</i>	54	—	58	6	X&Y:A	—	—	Wurster and Benirschke, 1967b
<i>Taurotragus oryx</i>	31 (♂) 32 (♀)	—	55-56	26	X:A; Y:A, translocated to an autosome	—	—	Hsu and Benirschke, 4(192), 1970 Taylor and Taylor, 1970 Hsu and Benirschke, 6(295), 1971
<i>Taurotragus euryceros</i>	33 (♂)	—	—	—	—	—	—	Wurster, 1972
<i>Tragelaphus angasi</i>	55 (♂) 56 (♀)	—	—	2	X&Y:?	—	—	Wurster and Benirschke, 1968b
<i>Tragelaphus scriptus</i>	33 (♂) 34 (♀)	—	56-58	24-25	X:A; Y:A, translocated to an autosome	—	South Africa	Hsu and Benirschke, 6(296), 1971 Wallace, 1977
<i>Tragelaphus spekei</i>	30	—	—	—	—	—	—	Wurster et al., 1968
<i>Tragelaphus strepsiceros</i>	31 (♂) 32 (♀)	—	55-56	26	X:A; Y:A, translocated to an autosome	—	—	Wallace and Fairall, 1967d Hsu and Benirschke, 6(297), 1971

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Speci- mens exam- ined	Country	Citation
Giraffidae								
<i>Giraffa camelopardis</i>	30	58	54	26	X:large SM; Y:small M	—	—	Wallace and Fairall, 1965
<i>Okapia johnstoni</i>	45	—	—	—	—	—	—	Hösl and Lang, 1970
Suidae								
<i>Phacochoerus aethiopicus</i>	34	—	—	—	—	—	—	Wallace and Fairall, 1967 ^b
<i>Sus scrofa</i>	36	—	60	26	X:M; Y:small M	—	—	McFee, 1965 Hsu and Benirschke, 1(39), 1967

PROBLEMS AND PRIORITIES OF RESEARCH ON THE TAXONOMY AND ECOLOGY OF AFRICAN SMALL MAMMALS

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Africa is still one of the research frontiers for studies of small mammal ecology and taxonomy. Yet for specialists from Europe and North America, transportation costs for persons and equipment is expensive and logistical support in Africa is costly. African scientists are not faced with such high expenses to begin or carry on research, but rather have to compete with other priorities in developing countries for funds that might be available for research.

African authorities formulating resource utilization plans are caught between factors of rapidly increasing populations, economic priorities, and potential short-term exploitive policies in attempting to implement long-term integrated land use policies which will allow for and include preservation of various representative ecosystems. Probably the destruction of entire ecosystems in Africa precipitates the greatest concern on the part of specialists studying the ecology and taxonomy of African small mammals. Time is growing critical if studies of many species are to be done adequately. In addition, changes required to insure adequate food supplies and protection from diseases add to the concern. Forest ecosystems, especially relict high forest, are becoming smaller and more isolated. Deserts of Africa are expanding.

Ecological and behavioral studies of small mammals in Africa are hampered by lack of financial support. Most ecological data have been collected opportunistically during other studies. Most population ecology studies are of short duration or seasonal in nature. Long-term monitoring studies of small mammal populations are few in number or include only short periods of trapping during the year. Long-term studies of resource division and habitat utilization have seldom been done. In all instances, quantitative analyses of data are marked by small sample sizes. Sufficient financial support must be made available to allow for long-range studies of up to 10 years' duration. This support must include salaries as well as logistical expenses.

Long-range field studies of behavior are needed for most small mammals. Some of those most ob-

viously offering opportunity for field observations are *Eidolon*, *Hypsignathus*, *Thryonomys*, *Cricetomys*, *Pedetes*, and various viverrid genera. Recent advances in night vision equipment make it possible to observe many of the nocturnally active genera.

Careful consideration should be given in selecting sites for ecological and behavioral studies. Among those in Africa offering the most pristine environmental conditions are the National Parks and Reserves. These areas, in addition to being more pristine, are staffed by people who have a vested interest in such studies. Laboratory or some other type of sheltered work space is usually available and security for laboratory and field equipment is usually better in these areas than elsewhere.

In most instances, African scientists doing research on small mammals are employed in other roles. Thus, they may only be able to conduct research during their spare time. Whenever possible, these scientists and their students should be included in research projects originating in Europe and North America. Such participation may be the only opportunity for them, especially the students, to learn specialized methodologies and techniques.

In recent years, a more active phase of interest has developed in studies of taxonomy of African small mammals. This upsurge of interest has been precipitated by the need for better taxonomic treatments of various groups of mammals on the part of ecologists, conservationists, agriculturalists, and medical zoologists. Even with the introduction of karyology in taxonomic studies in Africa, methodology still lags far behind some other areas of the world. Commitment of logistical support is needed so that all extant specimens, at least those in the major collections, can be included in taxonomic revisions. There must also be commitments of additional support so that those areas from which critical material is lacking can be visited in order to obtain any necessary missing data. Individuals must be encouraged to use the best and strongest statistical tests available to them in their taxonomic studies. Univariate statistical tests, including analyses of variance, must be a part of any taxonomic study

whenever possible. Ideally, multivariate statistical analyses should be included as well. Numerical taxonomic treatments of data in generic and specific revisions of African mammals must be encouraged.

Those individuals who are involved with taxonomic studies of African small mammals are well aware of which groups should be receiving the highest priorities in taxonomic research. However, a review of these groups will indicate the enormous task that remains to be done.

Among the traditional insectivores, one genus stands out in difficulty well above most other African small mammals. The genus *Crocridura* is undoubtedly the most complex of the insectivores and may be of any African mammal (Heim de Balsac and Meester, 1977). Sibling species are common, often sympatric in distribution, and study specimens are usually inadequate in number and widely distributed. Heim de Balsac and Meester (1977) list 85 species, but admit that this is a tentative compilation. Other insectivores deserving of treatment are the hedgehogs and golden moles at both generic and specific levels. Recent taxonomic arrangements of the latter by Simonetta (1968) and Meester (1974) indicate the differences of opinion that exist on the number and relationships of genera and species. Other genera, such as *Myosorex*, *Sylvisorex*, *Suncus*, and *Elephantulus* are deserving of additional attention but less critically so at this time.

Within the bats, a large number of genera are in critical need of taxonomic revision. Chief among these are *Epomops*, *Epomophorus*, *Rousettus*, *Taphozous*, *Rhinolophus*, *Hipposideros*, *Myotis*, *Nycticeius* (*sensu lato*), *Pipistrellus*, *Eptesicus*, *Scotophilus*, *Glaconycteris* (*sensu stricto*), *Kerivoula*, *Miniopterus*, and *Tadarida*. Some genera, such as *Rousettus*, *Pteropus*, *Emballonura*, *Plecotus*, *Nyctalus*, *Miniopterus*, and *Otomops*, have major Eurasian affinities as well, and taxonomic studies of these genera must consider both continents. Others, such as *Rhinolophus*, *Hipposideros*, *Pipistrellus*, *Eptesicus* and *Tadarida*, seem to separate into species groups on a continental basis.

The genus *Lepus* is in critical need of taxonomic treatment over the whole of Africa and Eurasia. In addition, a monographic study of both Recent and fossil genera of lagomorphs, including all continents of occurrence, should be encouraged.

The group showing the highest radiation of species in Africa is the rodents. Within this group, the squirrels contain the genera *Funisciurus* and *Par-*

axerus, which are critically in need of taxonomic revisions. Additionally, *Heliosciurus* is deserving of attention, with both *H. rufobrachium* and *H. gambianus* in need of studies of geographic variation. Studies of generic relationships are needed for both sciurid and anomalurid squirrels.

Among the genera of small rodents, the following African ones are in critical need of taxonomic revisions, utilizing every available method of establishing specific relationships: *Meriones*, *Gerbillus*, *Tatera*, *Taterillus*, *Gerbillurus*, *Mus*, *Aethomys*, *Acomys*, *Arvicanthis*, *Hybomys*, *Lemniscomys*, *Lophuromys*, *Pelomys*, *Mastomys*, *Praomys* (*sensu stricto*), *Hylomyscus*, *Grammomys*, *Cryptomys*, *Tachyoryctes*, *Steatomys*, *Dendromus*, *Otomys*, and *Graphiurus*. Attempts should be made to include in these studies other data than those traditionally included, for example, differences in life history, morphology of glans penes, sperm morphology, and karyotypes.

Additionally, studies of geographic and non-geographic variation are required for a number of currently recognized monotypic genera and some genera with only a few species. Without doubt, Ellerman (1940, 1941) and Ellerman et al. (1953) oversynonymized certain genera of rodents. Hubert (1978) has shown good evidence for two species in the genus *Saccostomus*. Other monotypic genera, which should receive critical review of geographic variation are *Dasymys*, *Oenomys*, *Rhabdomys*, *Thallomys*, *Uranomys*, *Malacothrix*, *Pedetes*, *Desmodillus*, and *Psammomys*.

Unfortunately, in many taxonomic revisions of African genera of rodents published in the past, insufficient attention has been given to non-geographic variation. Secondary sexual and age variation are present in nearly all rodents. Care must be exercised to compare only rodents of the same age in these taxonomic studies as these animals invariably continue to grow throughout most of their life.

In the remaining groups of small mammals, taxonomic studies are needed at the generic and specific levels for the prosimians, particularly *Galago*, the viverrids, especially *Genetta*, and the antelope genera *Cephalophus* (*sensu lato*), *Madoqua*, and *Gazella*. Hoeck (1978) has introduced a new approach in the study of the generic relationships of hyraxes and indicates as well the need for a comprehensive study of the genus *Procavia*.

Until better taxonomic treatments of many genera are available, statistical studies of the zoogeographic relationships of African mammals on a con-

tinental basis will be inadequate. Unfortunately, many zoogeographical studies, even regional ones, must make concessions for areas lacking adequate faunal surveys and for taxonomic confusion in certain genera.

Faunal surveys of African countries are becoming less common, primarily due to difficulties in obtaining necessary funding for such field work and maintenance of resulting collections. Yet, non-mammalogists are voicing an increasing desire for reports of the mammals of a given country. Even so, mammal surveys of certain regions would still be a valuable undertaking. The Ogoué Basin, the central Sahara, the western Sahara in the region formerly included in Spanish Sahara, the horn of Africa including Somalia, Ethiopia, and particularly Eritrea Province, the massifs on either side of the Rift in Central Africa, southern Zaire, and eastern Angola are in need of additional surveys for mammals.

Attention to endangered species of African mammals has focused mainly on large mammals and the primates. Many species of small mammals are so poorly known it is impossible to judge their status. Many obviously good species are known by less than 12 specimens, for example, *Leimacomys buttneri*, *Dendroprionomys rousseloti*, *Zinkerella insignis*, *Hylomyscus baeri*, and *Glauconycteris superba*.

Permits to conduct ecological and taxonomic studies in Africa are not required in all countries. Before issuing permits, some others require a complete and detailed proposal of the research to be submitted well in advance of the starting date; Kenya, for example, requires this information six months in advance. Without such permission, research conducted in these countries is illegal. For most countries, export of specimens requires a special permit or at least a letter of waiver. Unless all of the specialists cooperate in obtaining the necessary permission to conduct research and subsequent permits, requirements will become more restrictive and permission more difficult to obtain.

Individuals performing any type of research in Africa are well aware of the problems associated with economic growth versus conservation efforts. In dealing with the problems in this regard, the nations of Africa, although almost all are in a developing state, are no different from those of Europe and North America. However, the participants of the colloquium felt they would be remiss in their professional responsibility if they did not consider the destruction of various habitats, particularly forest ecosystems, and the mammals occurring there. The recommendations below received unanimous approval from the participants.

RECOMMENDATIONS OF THE PARTICIPANTS IN THE COLLOQUIUM ON ECOLOGY AND TAXONOMY OF AFRICAN SMALL MAMMALS SPONSORED BY CARNEGIE MUSEUM OF NATURAL HISTORY, 19–22 SEPTEMBER 1977

- I. The participants of the Colloquium on Ecology and Taxonomy of African Small Mammals recognize that these animals play an important ecological role in many natural and man-made habitats. Some species can be pests of agriculture and forestry as well as disease vectors in many parts of the continent. The Colloquium fully recognizes the high priority to be given to these problems.
- II. However, all of these species are vital to the functioning and maintenance of natural ecosystems. Furthermore, the role of many is totally unknown although probably very important in most instances. In view of the rapid decimation of natural habitats in Africa, particularly all types of natural forests, due to human encroachment and development of exotic tree plantations, the participants of the Colloquium

on Ecology and Taxonomy recommend that Institutions of all African countries and the International agencies concerned with these countries:

- A. Make every possible effort to conserve large and representative examples of all mature forest types, particularly montane and rain forests, which exist within their respective countries or areas of interest. These forest parks or nature reserves must be large enough (circa. 2,000 square km) to conserve viable populations of all animals and plants comprising the ecosystem, and must be completely protected against all forms of destructive exploitation. In some circumstances the remaining relict forest blocks are much smaller than the recommended size and in these cases an area as

- large as possible should be conserved. Where possible, boundaries of existing forest parks and nature reserves should be expanded to include sufficiently large and representative areas;
- B. Make every possible effort to develop educational programs in their schools and mass media for their general public which explain the value and necessity of forest conservation, and the importance of land-use programs based on long-term ecological goals rather than short-term exploitation;
 - C. Make every possible effort to develop integrated land-utilization policies based on sound scientific and long-term ecological principles, to overcome the competitive nature which usually prevails in the interactions of the various government departments concerned with land-utilization problems;
 - D. Make every possible effort to have all proposals for land, agricultural, and industrial development schemes reviewed by a board of ecologists before these proposals are implemented;
 - E. Encourage basic and long-term biological research on forest ecosystems. This research should include not only projects of theoretical importance, but those of relevance to the practical problems in the countries concerned, such as the control of pest species through the conservation of natural and mature forest habitats.
- III. The participants further concurred that integrated land-use policies based on long-term interests provide a more sound economic base than the short-term exploitive policies currently prevailing in many countries.
 - IV. Finally, and of primary importance, it was recognized that many of the problems associated with the implementation of these recommendations are directly related to the human population explosion.

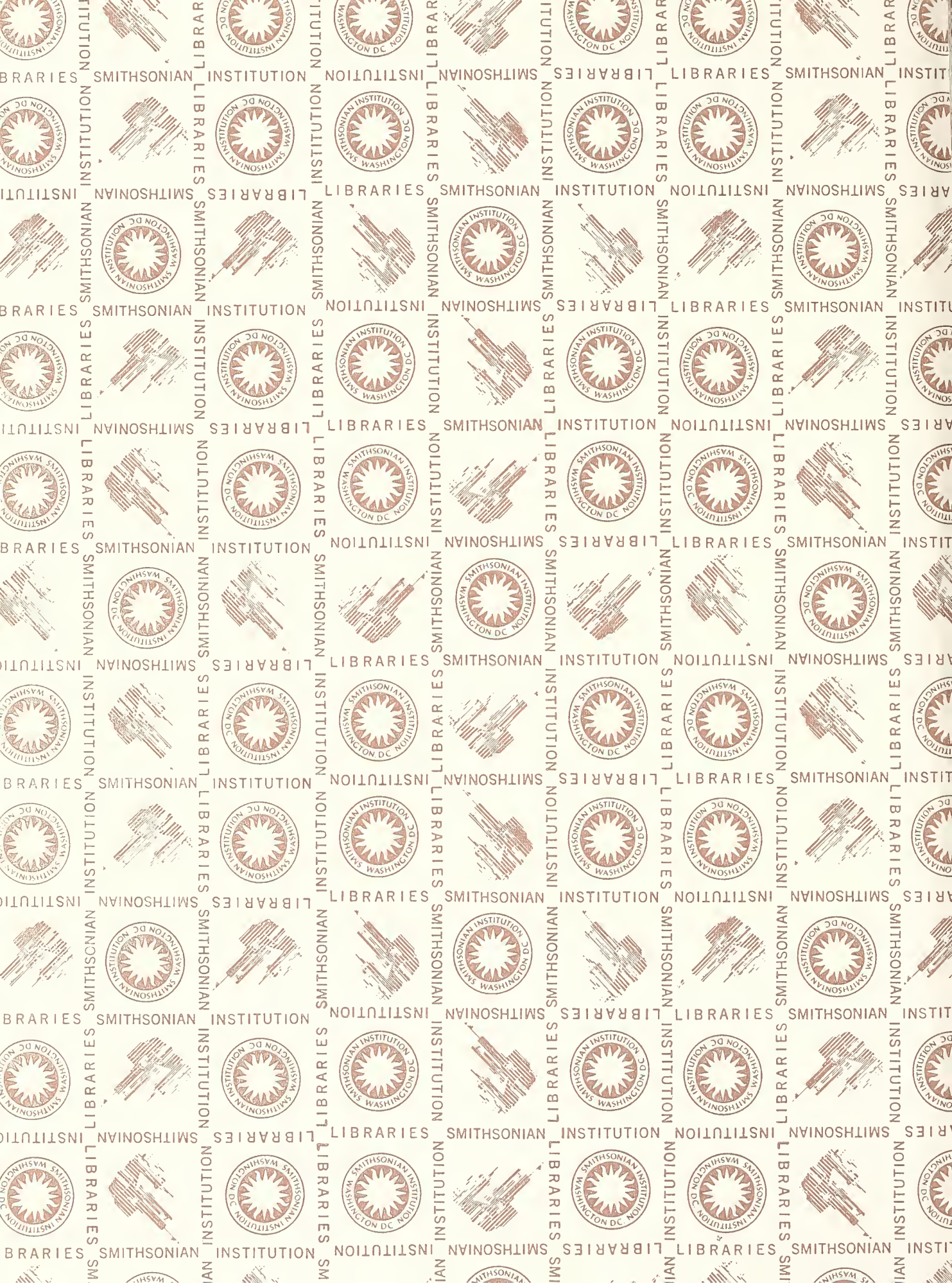
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